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WOOD, BARK, AND PITH ANATOMY OF OLD WORLD SPECIES OF *EPHEDRA* AND SUMMARY FOR THE GENUS

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ABSTRACT

Quantitative and qualitative data are presented for wood anatomy of 35 collections representing 22 Old World species of *Ephedra*; the survey of bark and pith anatomy is based on some of these species. Character-state ranges similar to those of the New World species are reported, although more numerous species show vessel absence in latewood. Little diminution in vessel diameter or density occurs in latewood of the eight species that are scandant or sprawling. Helical thickenings or sculpture occur in vessels of about a third of the Old World species, but these thickenings are clearly related to pits, often not very prominent, and rarely present in tracheids (alternative expressions characterize helical thickenings in the New World species). Helical thickenings are statistically correlated to xeromorphic wood features such as narrower vessels and fewer vessels per mm^2 of transection. Paucity of vessels is an indicator of xeromorphy (rather than abundance, as in dicotyledons) because tracheids, which have optimal conductive safety, are present instead of vessels. Near vessellessness is reported for *E. distachya* var. *monostachya, E. gerardiana,* and *E. monosperma.* A high degree of wood xeromorphy characterizes species of the highlands of Central Asia and the Middle East, where extremes of drought and cold prevail. A close approach to storied structure is reported in three species. Procumbent ray cells, absent at first, are produced as stems increase in diameter. Vessel element length also increases with stem size, and is not a phyletic indicator. Minute calcium oxalate crystals cover the outside of wood and bark cells, and suggest relationship to *Welwitschia* and perhaps conifers. A review of New World as well as Old World species reveals few species criteria, and these are mostly difficult to quantify. Primitive character states cannot be defined with certainty in the genus. Wood of *Ephedra* is like that of a vessel-bearing gymnosperm; parallelisms with dicotyledons may be caused by the vessel-bearing habit.

Key words: bark anatomy, ecological wood anatomy, *Ephedra,* Ephedraceae, Gnetales, growth rings, gymnosperms, vessellessness, wood anatomy.

INTRODUCTION

An earlier paper (Carlquist 1989) detailed wood and bark anatomy for the New World species of *Ephedra.* As noted there, wood anatomy has been studied for only a small number of species in the genus. Even for these few, descriptions of wood features are incomplete. Among the Old World species, data on wood anatomy have hitherto been presented for *E. distachya* by Thompson (1912), for *E. major* by Greguss (1955), and for four species of Israel and vicinity (*E. alata, E. aphylla, E. campylopoda,* and *E. foliata*) by Fahn, Werker, and Baas (1986).

As with the New World species, much new information and even new features have been uncovered by surveying *Ephedra* synoptically at the species level. Notable features include near vessellessness, diversity of growth-ring types, storying of tracheids, presence of minute calcium oxalate crystals on outside surfaces of wood and bark cells, and presence of helical sculpture in vessels and tracheids.

The present study surveys 35 collections representing 22 species. Of species recognized in recent studies, only *E. fedtshenkoi* Paulsen, *E. holoptera* H. Riedl, and *E. oxyphylla* H. Riedl are not included. These species all occupy very small

ranges in areas of difficult access (Riedl 1963; Bobrov 1968), so lack of material is understandable. The relatively complete representation of species in the present study has been made possible by the kindness of numerous individuals (see ACKNOWLEDGMENTS). Cultivated material has been employed for a number of species, in order to obtain wood samples larger than those generally available from herbarium specimens. The use of cultivated material for a number of species permits comparisons that could show the effect of climate or water availability on wood patterns. For some species, only herbarium material was available. The relatively small stems obtained from herbarium specimens are of interest in showing the nature of ontogenetic change in wood features such as ray histology and vessel element length.

The species in the present study would fall into the following infrageneric categories proposed by Stapf (1889):

Section I. *Alatae*
Tribe *Tropidolepides*
E. alata, E. lomatolepis, E. przewalskii, E. strobilacea.
Section II. *Pseudobaccatae*
Tribe *Scandentes*
E. altissima, E. aphylla, E. campylopoda, E. ciliata, E. foliata, E. fragilis, E. kokanica.
Tribe *Pachycladae*
E. intermedia, E. pachycladae, E. sarcocarpa.
Tribe *Leptocladae*
E. distachya, E. equisetina, E. gerardiana, E. major, E. monosperma, E. procera.

Species that have been described since Stapf's (1889) monograph and which have not been placed in the above system include *E. sinaica* and *E. sinica*; *E. lomatolepis* obviously belongs in *Alatae* on account of its dry bracts. Although I have reproduced Stapf's system as he gave it, section *Pseudobaccatae* must now be called section *Ephedra* because it contains the type species, *E. distachya*. Stapf's use of the term "tribe" is not in accord with current use: we would now use the term subsection. Wood patterns prove related to systematics at least for "tribe" *Scandentes*.

Patterns in wood anatomy are often referable to ecology, and the wood of *Ephedra* is of special interest in this regard even though *Ephedra* does not occupy a wide range of habitats. *Ephedra* is able to grow in dry habitats to which few angiosperms have adapted; *Ephedra* habitats range from dry to very dry. These habitats do show a wide range with respect to frost, however. The Old World *Ephedra* species range from near sealevel (species around the Mediterranean Sea) to nearly 5000 m (*E. gerardiana* in the Himalayas). Drought, heat, and frost are notably extreme in the highlands of Asia, and these species may be expected to show greater wood xeromorphy than do the lowland species, and in fact, they do.

In *Ephedra*, there are differences between species in wood anatomy that are probably related to habit rather than to ecology. Some species are large shrubs (data from Stapf 1889): *E. alata* (to 3 m), *E. strobilacea* (to 2 m). Some are very small shrubs: *E. gerardiana* varies from medium to very small. Stapf (1889) describes *E. monosperma* as less than 1 dm tall; its short upright stems, buried in sand, branch from underground horizontal rhizomes. This description applies

to *E. lomatolepis* also. Only a few New World species are scandent: *E. triandra* Tul., *E. tweediana* C. A. Meyer, and (climbing to a notable degree), *E. pedunculata* Engelmann. A larger number of Old World species qualify as climbing or sprawling: the group called *Scandentes* by Stapf (1889) as shown above. Species not mentioned in this paragraph are medium-sized shrubs.

The fact that some specimens were taken from herbarium specimens (and therefore are of limited size), whereas other specimens were field collected and represent stems of larger diameter, permits study of how wood features change ontogenetically. Features of potential interest are vessel diameter, vessel density, vessel element length, and ray histology. The specimen diameters (Table 1, column 1) are, in general, a good guide to age of wood sample. Only in exceptional instances is this not true. For example, one can see in the collection *E. gerardiana, Ludlow 4074* (Fig. 12, 13), that numerous very narrow growth rings are present, so that this sample—from an old high montane subshrub—represents an older stem than do much larger wood samples of *Ephedra.*

Wood anatomy has traditionally been considered a source of systematic information. Indeed, there are distinctive features in wood anatomy of dicotyledons and even conifers that have conventionally been used for wood identification. Consequently, there has been a tendency to regard comparative wood anatomy as a rich source of systematic information. Work on wood anatomy during the past two decades has shown that many wood patterns are correlated with ecology and habit of particular woody species rather than their systematic relationships. In any woody group there is a residue of features distributed with respect to a taxonomic system but not readily correlated with ecology. These can be regarded as of systematic significance. This residue of features is small in *Ephedra,* but a few characters may be cited.

At a different level of magnitude, a few wood features prove of considerable interest in analyzing the relationships of *Ephedra* to other Gnetales and of Gnetales to angiosperms. Is the wood of *Ephedra* more like that of a conifer or an angiosperm? If some resemblances to angiosperms are present, do these signify relationship, or are they the parallelisms that would be expected in a vessel-bearing gymnosperm that confronts physiological considerations similar to those in vessel-bearing angiosperms? *Ephedra* is a genus of exceptional interest with respect to these questions. Although authors have held that the wood of *Ephedra* (and other Gnetales) is clearly gymnosperms (Thompson 1918; Bailey 1944), some authors have demurred. Muhammad and Sattler (1982) have cited "scalaroid" perforation plates—scarce in both *Gnetum* and in dicotyledons—as evidence of relationship. The work of recent cladists (see discussion section at the end of this paper) has also claimed more similarities between Gnetales and angiosperms than data from wood anatomy would suggest. Although one may properly say that wood anatomy will not solve this problem, wood data based on a small number of species of *Ephedra* and *Gnetum* cannot be considered reliable. Consequently, I have undertaken a study of comparative wood anatomy of Gnetales at the species level.

MATERIALS AND METHODS

There is no study approximating a monograph of the Old World species of *Ephedra* since Stapf's (1889) coverage of the genus as a whole. I have used Stapf's treatment as a basis, but taken into account recent treatments, especially those of

Table 1. Wood characteristics of *Ephedra*.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
E. alata Decaisne	*Harris 26-III-1960*	5	0	79	35	755	2.3	1.8	13.0	12.0	.12	754	0	—	793	3.5	2.3
E. altissima Desf.	*SJRw-12725*	42	n	113	44	1167	2.4	2.4	11.6	15.3	.24	1471	0	—	4164	4.9	3.4 u
E. altissima	*Hort. Bot. Nikitensis*	7	n	154	34	809	2.5	1.9	8.2	11.2	.12	829	0	192	1334	4.0	2.8 u
E. aphylla Forssk.	*Cambridge U. Bot. Gard.*	8	n	104	31	502	2.8	1.6	9.5	9.8	.07	543	0	146	878	4.6	2.8 u
E. aphylla	*SJRw-12724*	32	n	98	46	768	1.8	2.5	12.9	17.4	.30	805	0	146	1666	8.4	2.5 u
E. campylopoda C. A. Mey.	*Davis 18067*	3	n	338	24	606	1.8	1.5	5.8	9.9	.05	670	0	—	1635	3.7	1.3
E. ciliata C. A. Mey	*Grant 15309*	7	F, N	99	26	562	2.3	1.9	11.3	12.0 14.0	.13	587	0	—	729	4.5	2.4 U
E. ciliata	*Koelz 13087*	8	F, N	198	34	597	1.4	2.2	9.1	11.6	.28	707	0	135	600	3.1	2.5 U
E. distachya L. var. *distachya*	*Mukidzhanyam 13-VII-1962*	4	0	104	27	683	2.2	2.2	14.9	9.2	.16	729	+	—	481	4.1	3.4 U
E. distachya var. *monostachya* (L.) Stapf	*Cambridge U. Bot. Gard.*	5	0	19	21	588	2.1	1.5	10.3		.01	680	++	—	1218	3.8	2.4
E. equisetina Bunge	*Elias 9746*	21	0	82	38	627	1.8	2.3	15.3	11.0	.12	671	+	—	2238	5.8	3.5 u
E. equisetina	*Elias 9840*	14	0	110	35	556	2.0	2.4	15.2	11.2	.18	632	+	—	2319	4.6	4.0 u
E. equisetina	*Elias 10067*	13	0	97	30	697	1.8	1.9	14.9	11.3	.14	766	+	—	704	4.3	3.0 U
E. foliata Boiss.	*SJRw-37203*	28	n	125	42	724	3.0	2.5	12.4	17.1	.36	722	0	264	434	4.1	2.3 U
E. fragilis Desf.	*Palermo Bot.* Gard.	15	n	68	49	979	2.5	2.3	13.6	16.6	.11	1020	0	262	2701	4.9	1.5 u
E. fragilis	*Cambridge U. Bot. Gard.*	5	F, n	72	38	668	2.2	2.0	10.2	13.8	.11	831	0	—	4888	4.8	2.2 U
E. gerardiana Wall.	*Freitag 1425*	5	0	49	24	515	1.6	1.7	10.8	10.1	.04	515	0	—	837	3.8	2.2
E. gerardiana	*Ludlow 4074*	7	0	1	28	406	2.2	2.0	7.7	9.2	.00	504	+	—	1331	?	<1 U
E. gerardiana	*Polunin 884*	7	F, 0	15	27	585	2.0	1.4	10.0	8.8	.01	650	+	324	828	2.6	2.4 U
E. intermedia Schrenk	*Hort. Bot. Nikitensis*	5	n	92	35	578	2.2	1.9	8.2	13.2	.10	680	0	126	601	2.6	2.3 U
E. intermedia	*Tashkent Bot. Gard.*	12	0	72	35	556	2.0	2.4	15.3	10.9	.10	603	0	156	1294	4.3	2.4 u
E. kokanica Regel	*Hort. Bot. Nikitensis*	11	n, N	150	36	491	2.2	1.8	7.4	16.5	.24	620	0	165	681	3.6	2.6 U
E. kokanica	*Elias 9742*	5	n	148	48	478	2.2	2.5	10.3	14.0	.23	660	0	169	779	2.4	2.0
E. lomatolepis Schrenk	*Morefield 5133*	3	F,0	139	30	593	2.3	1.9	13.1	11.7	.20	721	+	—	826	3.8	2.4
E. major Host	*Stainton 8250*	9	N, 0	92	34	566	2.3	2.3	13.0	11.3	.12	672	0	—	775	3.3	2.5 u

Table 1. Continued.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
E. monosperma C. A. Mey.	*Elias 7655*	12	0	12	27	435	2.3	1.7	10.8	7.8	.01	632	++	—	1724	?	<1
E. pachyclada Boiss.	*Freitag 3424*	3	F, 0	23	29	496	2.2	1.3	9.6	8.3	.01	646	0	—	2646	3.0	2.6
E. procera F. & M.	*Mukidzhanyam 27-IV-1962*	6	0	57	31	581	2.4	1.7	12.3	11.8	.08	656	0	—	473	7.6	4.0 U
E. procera	*Cambridge U. Bot. Gard.*	9	0	83	33	537	2.2	2.3	13.3	11.2	.11	569	0	—	924	3.9	3.2 u
E. przewalskii Stapf	*Morefield 4991*	18	N, 0	87	37	652	2.2	2.3	19.7	10.7	.15	736	++	—	832	4.0	3.0 u
E. przewalskii	*Morefield 4992*	8	0	46	30	676	2.2	1.8	16.8	10.7	.07	788	++	—	653	3.5	4.0 U
E. sarcocarpa Aitch. & Hemsl.	*Freitag 14017*	4	0	39	36	524	2.4	1.8	12.4	10.6	.04	774	++	—	621	2.8	3.5 U
E. sinaica H. Riedl	*Schmida 15-VIII-1974*	7	N	66	27	711	2.0	1.7	13.6	10.3	.07	742	0	—	802	3.3	2.4
E. sinica Stapf	*Liston 835-8*	8	0	39	27	472	2.0	2.2	12.1	12.0	.05	596	++	—	1324	4.6	2.0 u
E. strobilacea Bunge	*Ashirova 23-IV-1958*	8	N, 0	35	32	527	2.0	2.1	12.9	11.3	.04	617	++	—	642	3.2	2.4 U
Collections averaged				89	32	619	2.2	2.0	11.9	11.8	.12	691		190	1326	4.1	2.7

Key to columns: 1, diameter of sample excluding bark, mm; 2, latewood vessels compared to earlywood vessels in growth rings (F = vessels fewer, N = vessels appreciably narrower, n = vessels only slightly narrower, 0 = vessels absent); 3, mean number of vessels per mm^2; 4, mean vessel diameter at widest point, μm; 5, mean vessel element length, μm; 6, mean vessel wall thickness, μm; 7, mean number of series of perforations per perforation plate; 8, mean number of perforations per perforation plate; 9, mean diameter of perforations, μm; 10, mean area of perforations per mm^2 of transection, mm^2; 11, mean tracheid length, μm; 12, helical thickenings in vessels or tracheids (++ = conspicuously present, + = faintly present, 0 = absent); 13, mean height of uniseriate rays, μm; 14, mean height of multiseriate rays, μm; 15, mean width of multiseriate rays at widest point, cells; 16, mean wall thickness of ray cells, μm; ray histology (upper case = predominant cell type or types, U = upright, S = square, P = procumbent). For further information, see Materials and Methods.

Riedl (1963) for Iran and surrounding areas, and Bobrov (1968) for the U.S.S.R. *Ephedra sinaica* has been credited in accordance with Riedl's (1980) description of this species. A few species concepts not uniformly recognized in floras have been used here, notably *E. major* and *E. kokanica.* Material applied as *E. alte* C. A. Meyer is termed *E. aphylla* here; Danin and Hedge (1973) have demonstrated *E. alte* to be nomenclatural synonym of *E. aphylla.* Authors of binomials of the species studied are cited in Table 1.

Material was available in dried form except for the Elias collections of *E. equisetina* and *E. intermedia,* which were preserved in formalin-acetic-alcohol. Dried specimens were boiled in water and then stored in aqueous 50% ethyl alcohol. Woods were sectioned on a sliding microtome without softening except for *E. przewalskii.* The wood of this species is so hard that treatment with ethylene diamine was invoked. The treatment used was briefer in time than that recommended by Kukachka (1977) in order to avoid the tendency of ethylene diamine to swell lignified cell walls if applied for more than a day or two. Sections for study by means of light microscopy were stained in safranin and counterstained with fast green to various degrees. Fast green is excellent for demonstrating presence of tori and other pit membrane portions; thereby the bordered or nonbordered nature of pits could be ascertained readily. Some unstained sections were placed between glass slides in order to dry and flatten sections. These sections were then studied with an ISI WB-6 scanning electron microscope after coating with gold.

Presence of tori in pits as seen in transections permitted me to determine whether an end wall of a tracheary element bears pits (and is thus a tracheid) or perforations (in which case it is a vessel element). Using this method, I could demonstrate that vessel elements of *Ephedra* rarely have a lumen diameter less than 25 μm; no vessel element lumina smaller than 20 μm in diameter were observed. The nearly vessellessness nature of wood in several species was ascertained by means of identification of tori in end-wall pitting. The minimum diameter of a perforation in a perforation plate of *Ephedra* appears to be about 10 μm, perhaps a deep-seated feature of *Ephedra* wood based on the relatively great size of circular bordered pits on end walls of *Ephedra* tracheids. Tracheids have large bordered pit pairs on tracheid to tracheid contacts, smaller but definitely bordered pit pairs on tracheid to fiber-tracheid contacts. The term "fiber-tracheid" is used here for nucleated nonseptate fibriform cells with walls nearly as thick as those of tracheids and with pits vestigially bordered or simple, although some authors have used the term "parenchyma" for these cells. Reasons for usage of the term "fiber-tracheid" in *Ephedra* have been offered in my earlier paper (Carlquist 1989). Both fiber-tracheids of this sort and parenchyma strands of the sort found in dicotyledons coexist in wood of some species of *Gnetum.* In some species of *Ephedra* (*E. kokanica,* Fig. 31), one can find both fiber-tracheids and two-celled strands of parenchyma. Parenchyma consisting of strands of two cells is extremely rare or absent in all species of *Ephedra* according to my observations, contrary to the descriptions of Fahn et al. (1986), who attribute such parenchyma to all of the species they studied. They do not mention nonsubdivided fiber-tracheids, which perhaps they include in the concept of parenchyma.

Vessel element diameter (Table 1, column 4) is measured as lumen diameter at widest point. Both earlywood and latewood tracheids were selected for measurement of tracheid length, although in macerations earlywood tracheids are

shorter than latewood tracheids, as mentioned in a later section. Tracheids in macerations were identified on the basis of their large circular bordered pits. Measurements are not presented for uniseriate ray height if uniseriate rays are scarce in a collection; uniseriate rays do not comprise more than 20% of the rays in any of the Old World species. Rays two cells wide or wider are considered multiseriate rays. Quantitative features are based on 20 to 25 measurements per feature except for vessel wall thickness, tracheid diameter at widest point, tracheid wall thickness, and ray cell wall thickness. For these features, conditions judged to be typical were selected for measurements. Wall thickness is not measured on the basis of the angular corners of a cell, but the thinner portion between corners. In all matters of terminology, the usages in the earlier paper (Carlquist 1989) were followed.

Localities for specimens are as follows: *E. alata* (*Harris 26-III-1960,* E), Tunisia; *E. altissima* (*SJRw-12725*), Algeria; *E. altissima* (*cultivated in Hortus Botanicus Nikitensis, Yalta*); *E. aphylla* (*cultivated in the Cambridge University Botanic Garden*); *E. aphylla* (*SJRw-12724*), banks of the Indus River, India; *E. campylopoda* (*Davis 18067,* RSA), Lastos, Karpathos, Greece; *E. ciliata* (*Grant 15309,* RSA), 30 km N of Kahurak, Baluchistan, Iran; *E. ciliata* (*Kolez 13087,* W), Teshkan, 2000 m, Badaksh, Afghanistan; *E. distachya* var. *distachya* (*Mulkidzhanyam 13-VII-1965,* RSA), Nyuvadi, Megrinsky Region, Armenian SSR; *E. distachya* var. *monostachya* (*cultivated at Cambridge University Botanic Garden*); *E. equisetina* (*Elias 9746,* RSA), Aktash, 70–80 km NE of Tashkent, Tien Shan Mts., Uzbek SSR; *E. equisetina* (*Elias 9840,* RSA), 80 km N of Tashkent, Uzbek SSR; *E. equisetina* (*Elias 10067,* RSA), 55 km N of Dushanbe, Hissar Range of Pamir-Alay Mts., Tajik SSR; *E. foliata* (*SJRw-37203*), India; *E. fragilis* (*cultivated in the Palermo Botanic Garden, Palermo, Sicily, Italy*); *E. fragilis* (*cultivated in the Cambridge University Botanic Garden*); *E. gerardiana* (*Freitag 1425,* KASSEL), Bini-Dara-al, Kotal, Afghanistan; *E. gerardiana* (*Ludlow 4074,* E); Between Kala and Samada, 4750 m, U Province, southeastern Tibet; *E. gerardiana* (*Polunin 804,* E), Jumea, 2750 m, Nepal; *E. intermedia* (*cultivated at the Hortus Botanicus Nikitensis, Yalta); E. intermedia* (*cultivated at the Tashkent Botanic Garden*); *E. kokanica* (*cultivated at the Hortus Botanicus Nikitensis, Yalta*); *E. kokanica* (*Elias 9742,* RSA), cultivated at the Tashkent Botanic Garden, Uzbek SSR: *E. lomatolepis* (*Morefield 5133,* RSA), 48 km NNW of Fukang, Xinjiang, Uygur Autonomous Region, W. China; *E. major* (*Stainton 8250,* RSA), Artvin, Artvin Province, Turkey; *E. monosperma* (*Elias 7655,* RSA), W. Sajan Mts., Tuva Autonomous Republic, USSR: *E. pachyclada* (*Freitag 3424,* KASSEL), southern Kattawaz, Zakira Mts., W. Wazi Khwa, Afghanistan; *E. procera* (*Mulkidshanyam 27-IX-1962,* RSA), Khosrovsky Forest, Vedinsky Region, Armenian SSR: *E. procera* (*cultivated at the Hortus Botanicus Nikitensis, Yalta*); *E. przewalskii* (*Morefield 4991,* RSA), Tarim Basin, Xinjiang Uygur Autonomous Region, western China; *E. przewalskii* (Morefield 4992, RSA), Tarim Basin, Xinjiang Uygur Autonomous Region, western China; *E. sarcocarpa* (*Freitag 14017,* KASSEL), southern Kattawaz, Zakira Mts., western Wazi Khwa, Afghanistan; *E. sinaica* (*Shmida 15-VIII-1974*), Gebel Abas-Pasha, Sinai, Egypt; *E. sinica* (*Liston 835-8*, RSA), north slope of Bogda Shan, Xinjiang Uygur Autonomous Region, western China; *E. strobilacea* (*Ashirova 23-IV-1958*), 20 km N of Bakharden, central Kara-kum Desert, Turkmenian SSR.

ANATOMICAL DESCRIPTIONS; WOOD ANATOMY

Growth Rings

Growth rings are illustrated in Figure 1–14 as well as cited in Table 1. This account of growth-ring types is based upon the presentation used for the New World species (Carlquist 1989). Note should be taken of the fact that within a single stem, more than one growth-ring type can occur, depending on the severity of the season. However, the shifts are predictable (e.g., one cannot find the first type combined with the fifth type in a particular wood). The types observed are as follows:

1. Vessels only slightly narrowed in latewood, but not noticeably fewer. This type is shown for *E. fragilis* in Figure 1, as well as for *E. altissima* in Figure 36, 37, and 38. Narrowing of tracheids in a radial direction occurs at the ends of growth rings, but there is only a little narrowing of the vessels, and no perceptible diminution of vessel numbers until the formation of those few layers of narrow tracheids. In fact, if the narrow tracheids were not formed, one probably would not be able to say growth rings were present at all. This growth-ring type characterizes *A. altissima, E. aphylla, E. campylopoda, E. foliata, E. fragilis,* and *E. kokanica,* all denoted by "n" in Table 1, column 2. All of these are scandent or scrambling species.

2. Vessels appreciably narrower in latewood than in earlywood ("N" in Table 1, column 2). This condition is shown in Figure 3 and 4 for *E. kokanica* (*cult. Hort. Bot. Nikitensis*). Woods belonging to six species showed this growth-ring type, either in combination with type 1 (*E. kokanica*) or type 4 (*E. major*).

3. Vessels appreciably fewer in latewood than in earlywood. Although the materials studied of Old World species of *Ephedra* did not yield a sample in which this type exclusively was represented, occasional growth rings of this type could be found. One is illustrated here for *E. gerardiana* (*Polunin 884*) in Figure 10. This growth ring was found in combination with type 2 (*E. ciliata, E. fragilis*) or type 4 (*E. gerardiana, E. lomatolepis, E. pachyclada*). This growth-ring type may be relatively uncommon (in comparison to its somewhat greater frequency in the New World species) because type 4, which seemingly represents an adaptation to more drastic climatic conditions, is relatively more common.

4. Vessels absent in the latter halves of growth rings ("0" in Table 1, column 2). The transection of wood of *E. equisetina* (Fig. 5) exemplifies this type clearly. The section of *E. przewalskii* (Fig. 6) also illustrates this type, although with less clarity because of the narrowness of the growth ring. If growth rings are very narrow because of a very dry growing season, latewood devoid of vessels may not be extensive.

5. Vessels absent or nearly so (examples designated by "0" only in Table 1, column 2, fall into this category if number of vessels per mm^2 is below 20). Four of the collections studied fall into this type: *E. monosperma* (Fig. 7), *E. distachya* var. *monostachya* (Fig. 8, 9), *E. gerardiana, Polunin 884* (Fig. 11) exemplifies this condition more than Figure 10, and *E. gerardiana, Ludlow 4074* (Fig. 12, 13). Of these, the samples of *E. distachya* var. *monostachya* (Fig. 8, 9) and *E. monosperma* have relatively wide growth rings. Extremely narrow growth rings characterize the collection *E. gerardiana, Ludlow 4074* (Fig. 12, 13). In this collection, some growth rings consist of a layer of earlywood tracheids followed by only one or

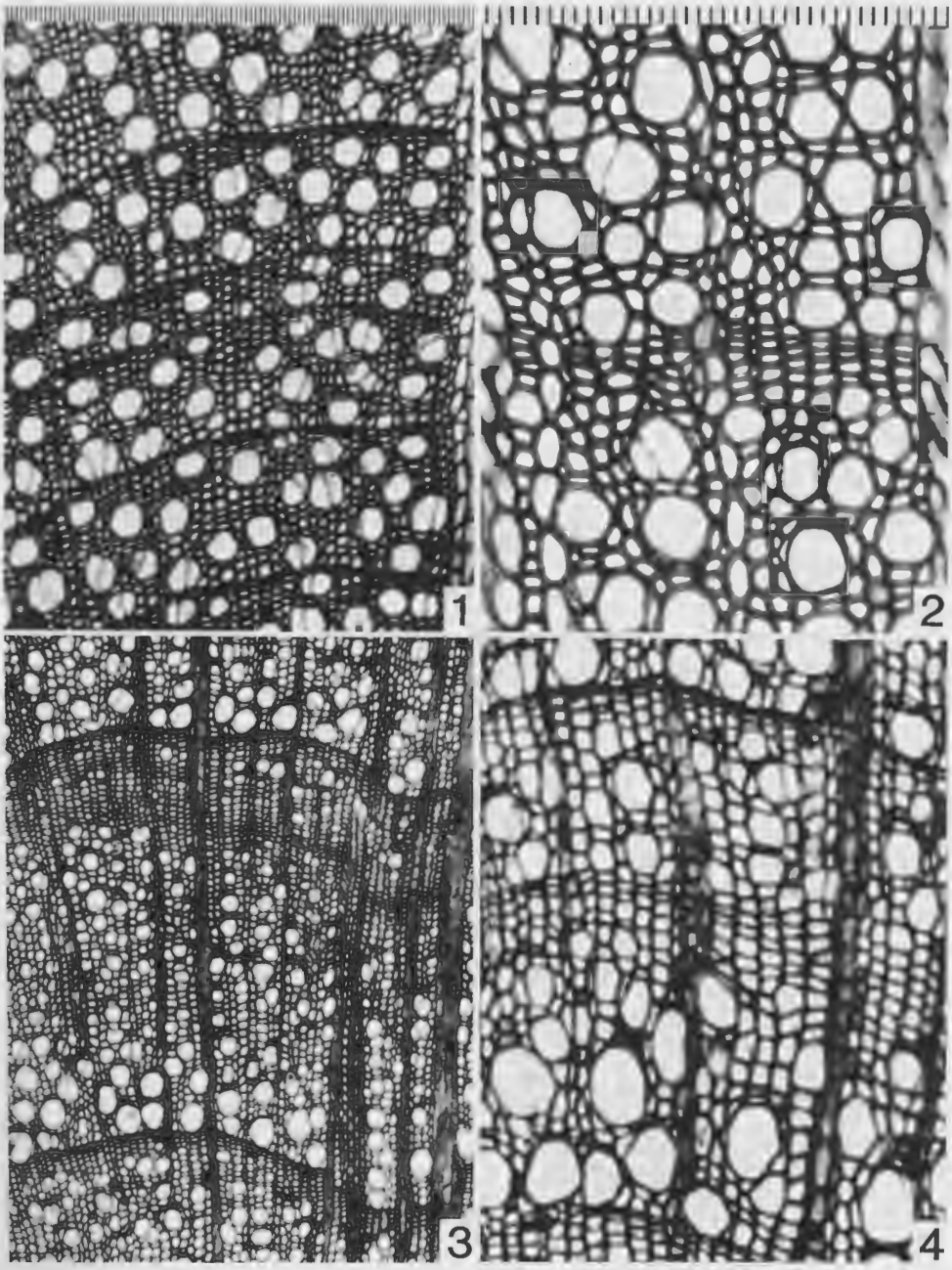

Fig. 1–4. Transections of *Ephedra* wood to show growth rings.—1. *E. fragilis* (*Palermo Botanic Garden*); five growth rings with little narrowing of latewood vessels are shown.—2. *E. altissima* (*SJRw-12725*); end of growth ring with little diminution in number or diameter of vessels; narrow tracheids and latewood.—3–4. *E. kokanica* (*Hortus Botanicus Nikitensis*).—3. Growth rings showing diminution in vessel diameter.—4. Growth ring, incorporating perhaps a "false growth ring" (narrow vessels followed by tracheids). (Fig. 1, 3, magnification scale above Fig. 1 [divisions = 10 μm]; Fig. 2, 4, magnification scale above Fig. 2 [divisions = 10 μm].)

two layers of latewood tracheids. This wood is the most nearly vesselless of the Old World species of *Ephedra,* and was cited in this regard in an earlier paper (Carlquist 1988). The plant represented by this collection was collected in a region with an extreme climate, the Tibetan plateau at 4750 m. The other nearly vesselless species also occur in localities well above sea level, in which the continental nature of the winters provides low minimum winter temperatures and relatively short growing seasons. In addition to the examples cited above, one can occasionally find in several of the Old World species of *Ephedra* an occasional growth ring that is vesselless. Vesselless first-year wood succeeded by vessel-bearing subsequent wood in subsequent growth rings is illustrated in Figure 14 for *E. equisetina* (*Elias 9746*). The entirety of the second year's growth ring in this sample is illustrated in Figure 32.

Vessel Density

Mean vessel density is reported in Table 1, column 3. The nearly vesselless species can easily be distinguished: they have a vessel density of less than 20 vessels per mm^2. In the remaining collections, vessel density ranges upward to 338 vessels per mm^2, and the mean for the collections is 89. Relatively high vessel densities characterize species in which there is little fluctuation in vessel diameter or density throughout a growth ring (Fig. 1, 2). The species with type 4 growth rings (vessels absent in latewood) have a relatively low vessel number of vessels per mm^2 (mostly from 35 to 100). Evidently the density of earlywood vessels, however great, does not "compensate" for the absence of latewood vessels (dense earlywood vessels do not produce, in these woods, a mean vessel density as great as that in the species with type 1 growth rings). Hypotheses that attempt to account for the various vessel density configurations are given in a terminal section of this paper.

Vessel Diameter

Figures for mean vessel diameter are given in Table 1, column 4. One may have the idea that vessel diameter should be roughly inverse to vessel density because of packing considerations. In dicotyledons, one finds considerable deviation from a straight line relationship (Carlquist 1975:183). There are many instances in which number of vessels falls well below what packing considerations would dictate, based on a particular vessel diameter. In species of *Ephedra* in which vessels are few or absent in latewood, and especially in nearly vesselless species, vessel density falls far short of what packing considerations would dictate for any given mean vessel diameter.

The mean vessel diameter for the Old World species of *Ephedra* is 32 μm. This would be a very narrow vessel diameter for a woody dicotyledon. In addition, the conductive area is somewhat smaller than the vessel diameters would suggest, because vessels in *Ephedra* deviate from circular outline frequently; they are often wider radially than tangentially (e.g., Fig. 3), and the widest lumen diameter has been used for measurements.

Vessel Element Length

Mean vessel element length of the Old World species ranges from 406 to 1167 μm. Mean vessel element length for all the collections of the present study is 619

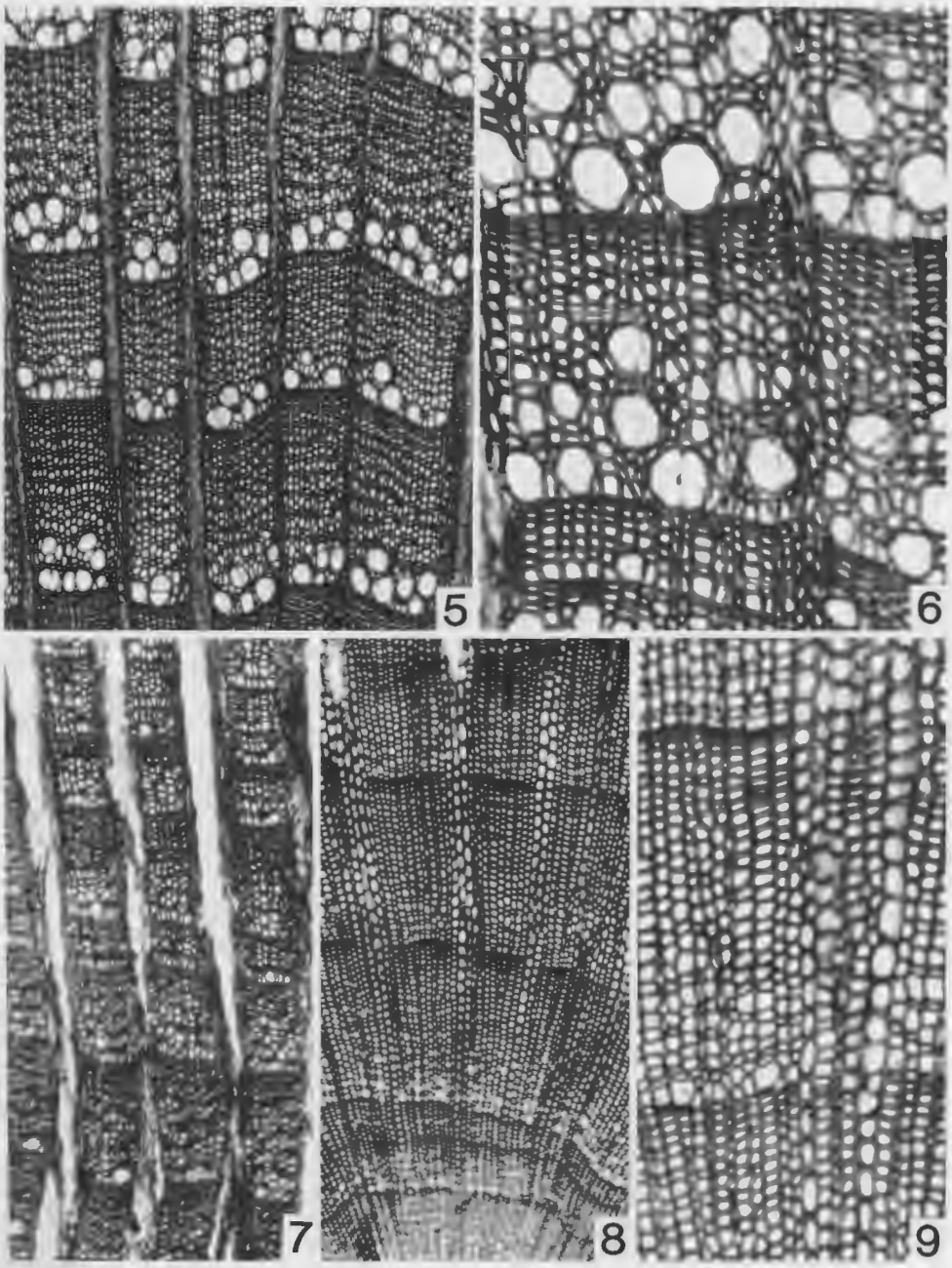

Fig. 5–9. Transections of *Ephedra* wood to show growth-ring types.—5. *E. equisetina* (*Elias 9746*), vessels present only in first portion of each growth ring.—6. *E. przewalskii* (*Morefield 4991*), vessels tend to be absent in latter portion of growth rings.—7. *E. monosperma* (*Elias 9655*), nearly vesselless wood; vertical rifts are ray areas with collapsed ray cells.—8–9. *E. distachya* var. *monostachya* (*Cambridge University Botanic Garden*).—8. Transection showing a succession of nearly vesselless but wide growth rings.—9. A growth ring (center of photograph) containing (at its beginning) two vessels. (Fig. 5, 7, 8, scale above Fig. 1; Fig. 6, 9, scale above Fig. 2.)

μm, which is shorter than that reported for the New World species (697 μm). The cause for this difference is doubtless the diameter of wood samples studied: smaller-diameter wood samples have shorter vessel element length (Carlquist 1989, Table 4), and more large-diameter samples were available for the study of the New World species. The longest vessel elements in the present study were observed in the largest-diameter sample studied, that of *E. altissima* (*SJRw-12724*). The shortest vessel elements were observed not in the sample with the smallest diameter, but in that of a very diminutive (and relatively old, with relation to sample diameter) shrub, the high-elevation collection of *E. gerardiana* (*Ludlow 4074*).

Vessel Wall Thickness

Vessel wall thickness averages 2.2 μm in the Old World species of *Ephedra* (Table 1, column 6), and the range within the collections is not very great. This degree of uniformity seems more interesting than the extremes, and no correlations between vessel wall thickness and otherwood features appear significant.

Perforation Plates and Lateral Wall Pitting

The foraminate perforation plates of Old World species of *Ephedra* are shown in Figure 15–19. Perforations are always clearly bordered. Exceptionally well-developed borders are shown for a narrow vessel of *E. major* in Figure 15. Even if borders are not wide or raised above the remaining wall surface, they can be seen readily if perforations are viewed in an oblique fashion (Fig. 16). Typically, perforations are very close to circular in outline. Where moderately crowded, the outlines may be somewhat transitional from circular to polygonal (Fig. 17). In two species with a sprawling (*E. ciliata,* Fig. 18) or scandent (*E. kokanica,* Fig. 19) habit, perforations are relatively large. Where perforations are large, there is more tendency for polygonal outline of perforations. Also, the perforations are often oval, wider radially (horizontally) than vertically.

The number of series of perforations per perforation plate is quantified in Table 1, column 7. If a perforation plate is only one perforation wide throughout, it was rated "1"; if two perforations wide at any point, it was assigned the value "2". Similar considerations were applied to three or four series. Interestingly, the mean number obtained in this way for the samples as a whole was 2.0. This means that on average, the perforation plate has two series along part or most of its length. In general, the widest vessels in *Ephedra* might be expected to have three or even four series of perforations, whereas the narrowest have only a single series of perforations.

Number of perforations per perforation plate can be quite readily counted, and the mean number per perforation is given for the collections in Table 1, column 8. Mean number of perforations per perforation plate in Old World species reaches a low of 5.8 in *E. campylopoda,* the stems of which available for study had very narrow vessels (averaging 24 μm in diameter). The highest mean number of perforations per perforation plate was recorded for *E. przewalskii* (*Morefield 4991*), 19.7. This is higher than the mean number recorded in any New World species of *Ephedra.* Although there is not a perfect correlation, there is a tendency for higher number of perforations per perforation plate to occur in species with greater mean vessel diameter.

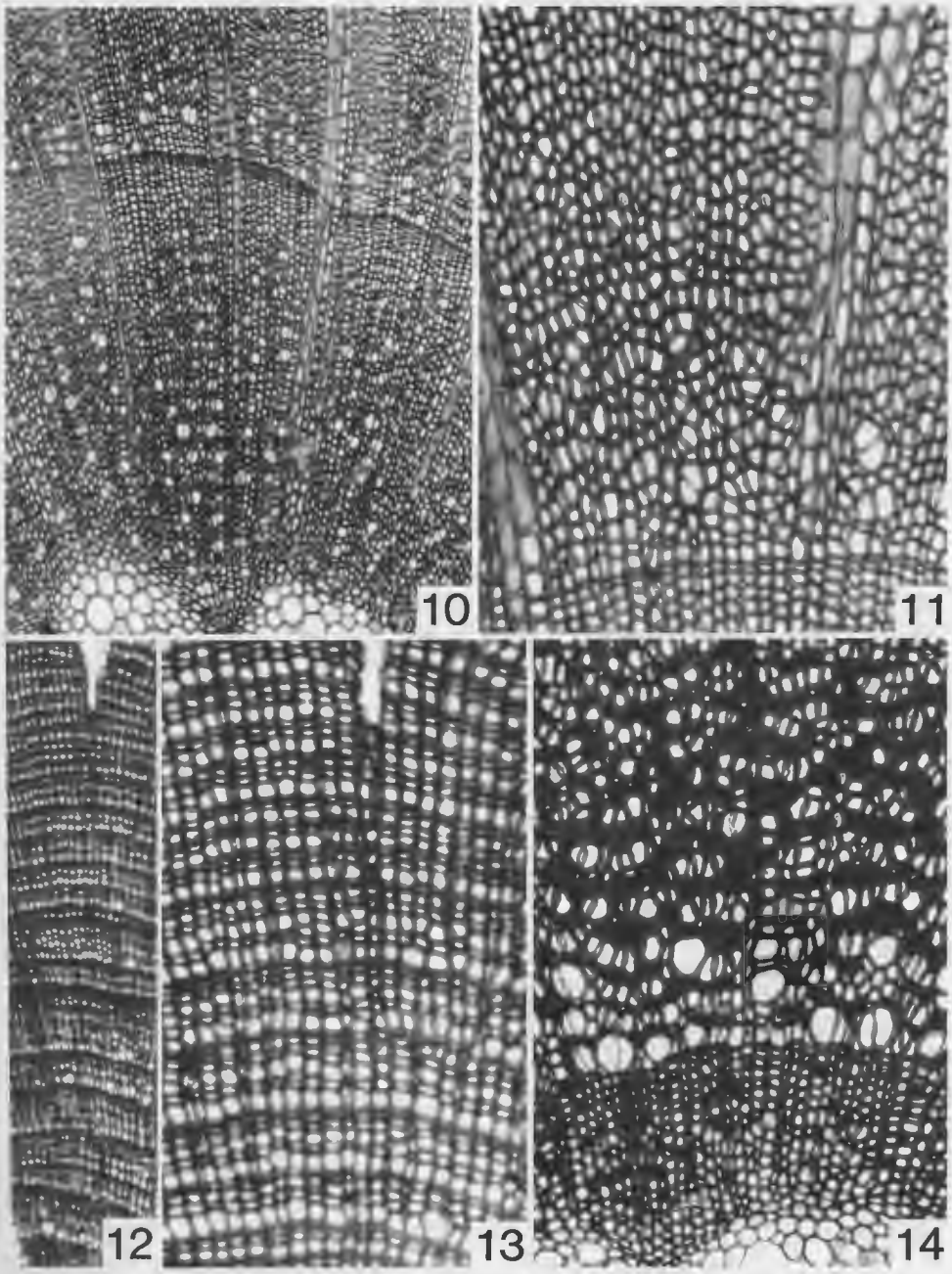

Fig. 10–14. Transections of *Ephedra* wood to show nearly vesselless conditions.—10–11. *E. gerardiana* (*Polunin 884*).—10. Pith and first two growth rings, showing very narrow vessels that become fewer in latewood.—11. Nearly vesselless wood portion (three probable vessels near beginning of growth ring).—12–13. *E. gerardiana* (*Ludlow 4074*).—12. Numerous growth rings (probably more than 25) in which few vessels occur.—13. Growth rings vey short; only one vessel shown (to left of numeral).—14. *E. equisetina* (*Elias 9746*), pith and two growth rings, the first of which is vesselless, the second of which begins with vessels. (Fig. 10, 12, scale above Fig. 1; Fig. 11, 13, 14, scale above Fig. 2.)

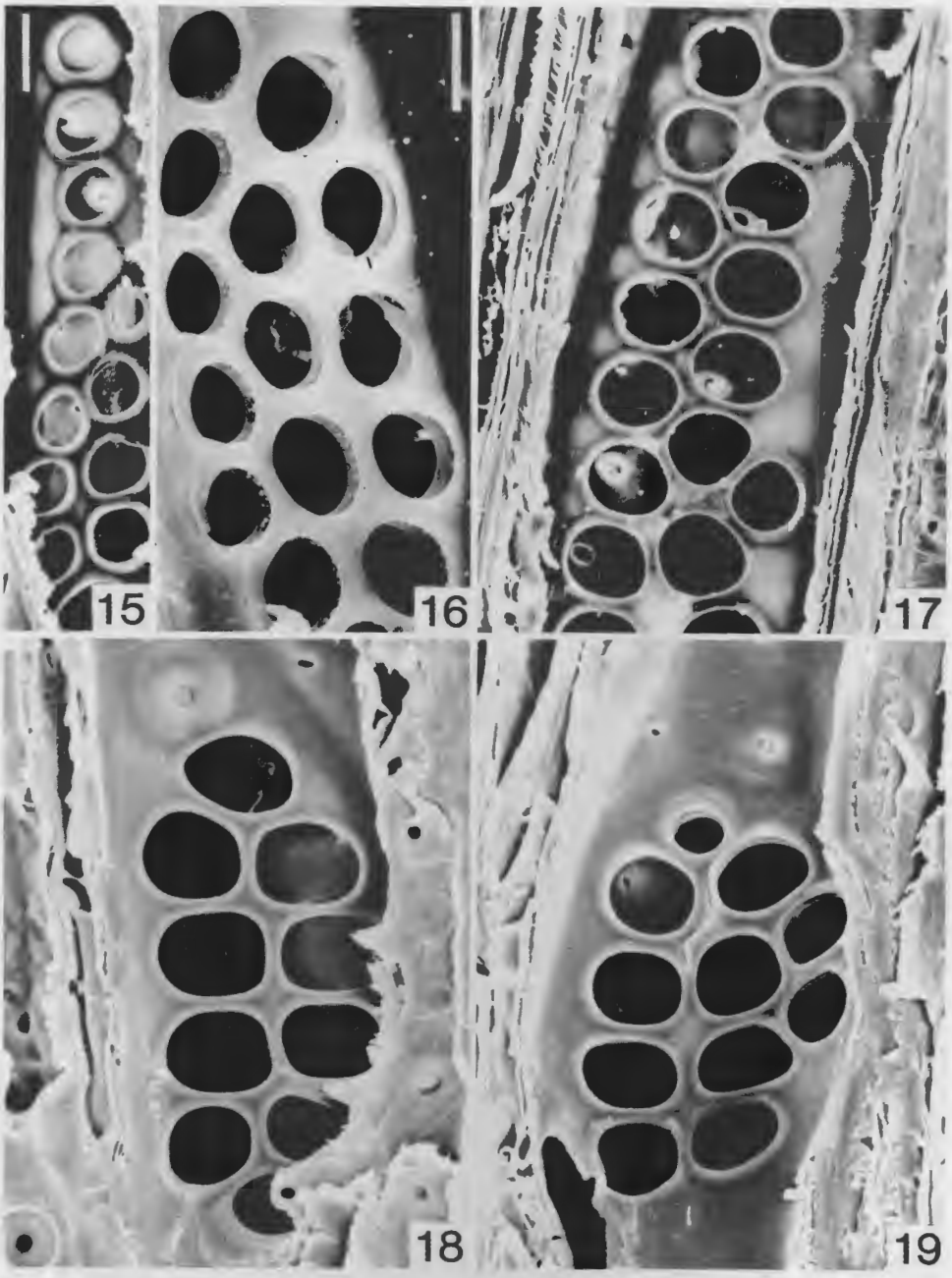

Fig. 15–19. SEM photographs of perforation plates of *Ephedra,* from radial sections of wood.—15. *E. major* (*Stainton 18280*), perforations with raised borders.—16. *E. przewalskii* (*Morefield 4991*), perforations viewed obliquely to show bordered condition.—17. *E. intermedia* (*Tashkent Botanic Garden*), three series of near-circular perforations.—18. *E. ciliata* (*Koelz 13087*), perforations large, radially widened.—19. *E. kokanica* (*Elias 9742*), perforations transitional between circular and polygonal shape. (Fig. 15, scale at top left [bar = 10 μm]; Fig. 16–19, scale at top right in Fig. 16 [bar = 10 μm].)

Mean perforation diameter (Table 1, column 9) shows a relatively great range, a range illustrated photographically in Figures 15 to 19. Perforations are narrow in the *E. major* plate shown (Fig. 15), intermediate in *E. przewalskii* (Fig. 16: note that the scale is slightly higher than for the remaining photographs on the page), and *E. intermedia* (Fig. 17). Relatively large perforations are illustrated for *E. ciliata* (Fig. 18) and *E. kokanica* (Fig. 19), two species which have a scrambling or ascending rather than upright habit. The data of Table 2 clearly shows the widest perforations (averaging more than 12 μm) in scandent species (*E. altissima, E. aphylla, E. ciliata, E. fragilis, E. kokanica*). Narrowest perforations (less than 9 μm) were recorded in *E. gerardiana, E. monosperma,* and *E. pachyclada.* The first two of these are small subshrubs.

As with the New World species of *Ephedra,* the quantitative expression relative to perforations that is most significant in terms of habit and habitat proves to be the mean total area of perforations per mm^2 of transection. This figure is calculated by multiplying the mean perforation radius squared times 3.14 times mean perforation number per perforation plate times mean number of vessels per mm^2. This figure (Table 1, column 10) offers a better representation of conduction characteristics of vessels than would vessel diameter or vessel number per mm^2, or even the mean vessel area per mm^2 (for reasons, see Carlquist 1989).

The mean total perforation area per mm^2 of transection differentiates the species quite markedly. The values range from almost infinitely small in the vesselless species (0.0006 in *E. gerardiana, Ludlow 4074*) to 0.36 (*E. foliata*). The significance of this gamut is discussed in terms of habit and ecology in a later portion of this paper.

Some instances of vessel elements with more than two perforation plates were seen. In these cases, branching of the vessel may be suspected. Number of perforations at one end might be expected to be virtually the same as the number of perforations at the other end of a normal vessel element in *Ephedra* because of flow considerations, but marked deviations in perforation number between the two ends could often be seen. Pits with reduced borders (Fig. 20, 21) may be present among the perforations in a perforation plate. What appears at first glance to be a perforation plate in Figure 20, because of the wide pit apertures and reduced borders, is actually an end wall of a tracheid that shows pit characteristics very similar to those of perforations. Perforationlike pits distributed within perforation plates of *Ephedra* were figured by Thompson (1912). In fact, in all species one can find tracheary elements showing degrees of transition between typical tracheids and typical vessel elements.

Lateral walls of vessels have pits with wide borders, much like those figured for conifer tracheids. These are vessel to tracheid pits. Pits between vessels and the living fiber-tracheids are definitely bordered, but the pits are smaller in diameter than vessel to tracheid or tracheid to tracheid pits. Greguss (1955) figures laterally elongate pit apertures on vessel walls for *E. distachya,* but these are, in my experience, infrequent; pit apertures are generally circular (Fig. 25), although some lateral widening may be seen in species in which helical thickenings occur on vessel walls (Fig. 26, 27).

Tracheids

Mean tracheid length is given in Table 1, column 11. The mean tracheid length for all collections (691 μm) is less than that for the New World species (765 μm).

The difference is probably attributable to the larger diameter of samples, on the average, in the specimens studied of New World species. Samples with larger diameter have greater tracheid length (Table 1).

Earlywood tracheids in the *Ephedra* collections studied here are often wide, with blunt ends; they are little longer than the vessel elements they accompany. Latewood tracheids are longer and more slender than earlywood tracheids. Earlywood and latewood tracheids cannot be readily separated from each other. In one instance, an attempt was made to measure the two categories separately; in *E. monosperma,* earlywood tracheids averaged 468 μm long, whereas latewood tracheids averaged 624 μm.

Mean tracheid length divided by mean vessel element length averaged 1.12 for the Old World species as a whole, a value virtually identical to that for the New World species (1.11). This ratio indicates little difference between tracheids and vessel elements with respect to elongation capability. In fact, a mean vessel element length longer than mean tracheid length was obtained for one collection (*E. foliata*) in the present study, and three in the earlier study (Carlquist 1989). Conceivably a larger sample size would have produced different results, but the closeness of the two cell types is the significant finding. Mean lengths of the two cell types were virtually identical in *E. alata.*

End walls of tracheids are provided with large pits close to each other (Fig. 22). The tori and threadlike margo strands illustrated for that species are much like those often figured for conifer tracheids, and certainly not like pit membranes of angiosperm tracheids. Tracheids of *Ephedra* have pits mostly on radial walls, as in conifers, less commonly on tangential walls except in latewood (Fig. 24). The radial width of tracheid walls of *Ephedra* accommodates only a single series of the full-sized bordered pits, which are rather large, like those of conifers (Fig. 20, 22). The radial width of latewood tracheids is less than the diameter of a typical bordered pit; this circumstance may account for pits that occur on tangential walls instead of radial walls in latewood.

Tracheids of *Ephedra* are mostly fusiform in shape. However, irregularities in wall outline as seen in macerations were evident in several species of *Ephedra* and are shown for *E. foliata* in Figure 23.

Fiber-tracheids

The cells termed fiber-tracheids here (parenchyma of some other authors) are nonseptate and contain one or more nuclei at maturity. They bear bordered pit pairs on contracts with tracheids. Pits between adjacent fiber-tracheids are small (about 2 μm in diameter); these pits are simple or nearly so. Fiber-tracheid to fiber-tracheid pits with vestigial borders were reported earlier, together with photographic evidence (Carlquist 1989). Vestigial borders may be more evident with SEM than with light microscopy. Reasons why these cells are called fiber-tracheids rather than parenchyma (as in Martens 1971) are discussed earlier. Thompson (1912) believed these cells result from a kind of tracheid dimorphism.

Grouping of the fiber-tracheids into patterns much like those of axial parenchyma in angiosperms is evident in *Ephedra* wood. Tangential grouping of a sort that would be called diffuse-in-aggregates in dicotyledon woods is illustrated here for *E. equisetina* (Fig. 24). Species in which "diffuse-in-aggregates" distribution of nucleated fiber-tracheids was observed include *E. altissima, E. aphylla, E.*

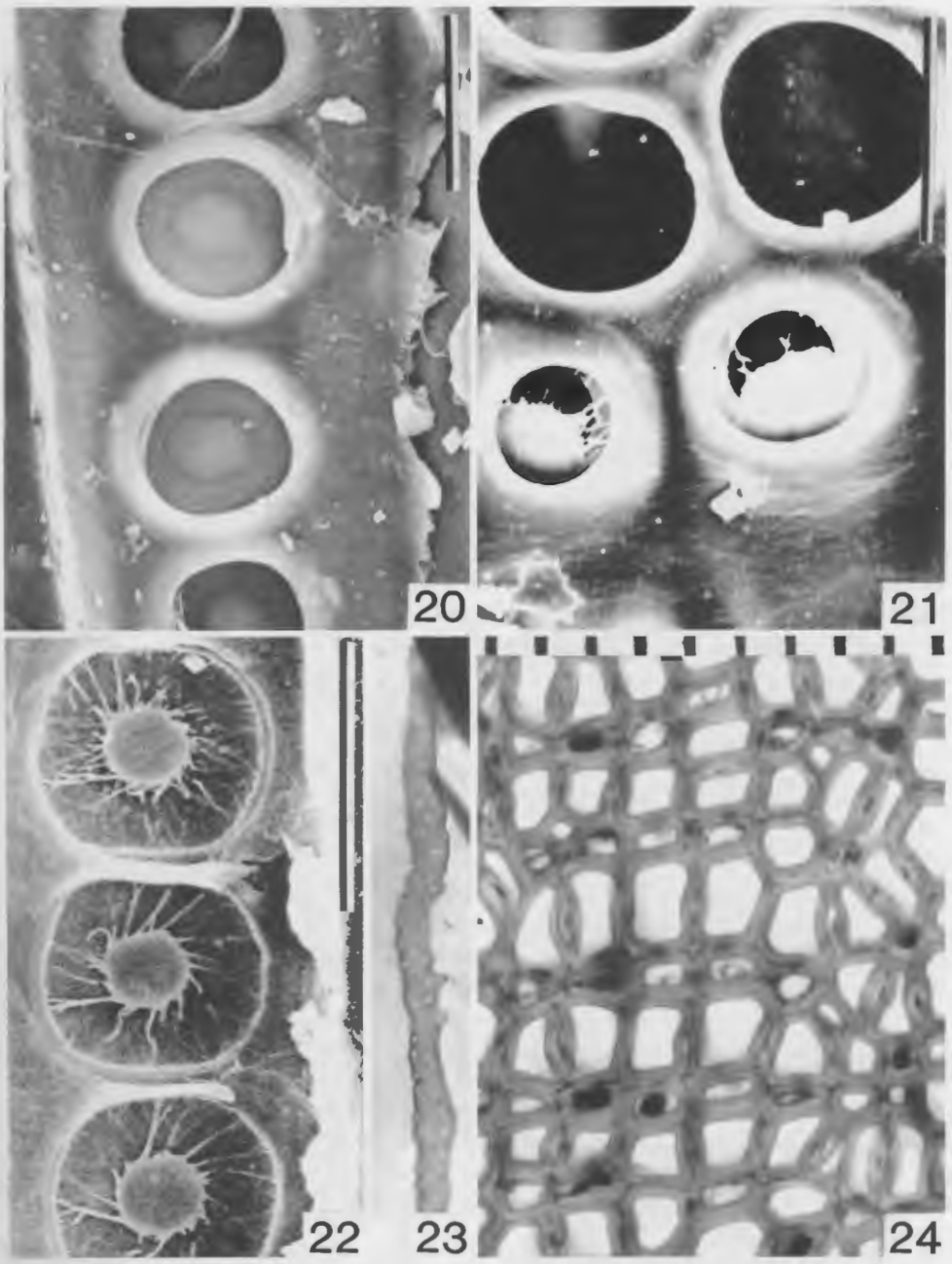

Fig. 20–24. Wood of *Ephedra*, showing details of tracheids, pitting, perforations.—20. *E. equisetina* (*Elias 9746*), tracheary element from radial section; wide apertures with vestigial borders like perforations, pit membranes with tori present.—21. *E. intermedia* (*Tashkent Botanic Garden*), portion of a perforation plate with two small pits at bottom (pit membranes ruptured).—22. *E. gerardiana* (*Polunin 884*), pits on end wall of tracheid, from radial section (tori and margo threads visible).—23. *E. foliata* (*SJRw-37203*), tracheid with irregular surface from maceration.—24. *E. equisetina* (*Elias 9746*), transection portion to show fiber tracheids (narrower cells, with contents), tracheids (wider cells without contents), and nature of pitting among cells. (Fig. 20–22, scale at top right in Fig. 20 [bar = 10 μm]; Fig. 23, scale above Fig. 2; Fig. 24, scale at top of Fig. 24 [divisions = 10 μm].)

distachya var. *distachya*, *E. equisetina*, *E. gerardiana* (*Freitag 1425*, *Ludlow 4074*), *E. intermedia*, *E. kokanica*, *E. lomatolepis*, *E. major*, *E. monosperma*, *E. procera*, *E. przewalskii*, and *E. sinica*. In Old World species not included in the preceding list diffuse distribution was much more common than diffuse-in-aggregates. In all species, some diffuse cells are present.

Fahn et al. (1986) report that fiber-tracheids ("parenchyma" in their usage) are "paratracheal scanty and apotracheal diffuse" for the four species they studied. My interpretation of the conditions they studied differs in that the fiber-tracheids adjacent to the vessels seem no more abundant to me than would be expected if random distribution of these cells throughout the wood occurred. Therefore, I prefer to consider that there is no paratracheal distribution of these cells in *Ephedra*.

Narrow bands of the fiber-tracheids (more than one cell wide) are illustrated here for *E. equisetina* in Figure 32. In this photograph, fiber-tracheids of the latewood have diffuse distribution, and the bands of cells are limited to earlywood subsequent to the first-formed vessels. I believe that the deposits of dark-staining compounds in this photograph serve as accurate indicators; the cells I am considering fiber-tracheids in that photograph are smaller in diameter and have slightly thinner walls than do the tracheids. Species in which narrow bands of fiber-tracheids were observed include *E. lomatolepis*, *E. procera*, and *E. sinica*. Apotracheal clusters of three to five fiber-tracheids were observed in wood of *E. distachya* var. *distachya* and *E. major*.

Wall Sculpture in Vessels and Tracheids

Helical sculpture in vessels is reported in Table 1, column 12. SEM photographs of vessel wall sculpture are presented in Figure 25–28. Where sculpture is more moderate ("+" in column 12), striae only a little raised above the wall surface may be seen, as illustrated for *E. equisetina* in Figure 25. More marked helical thickenings in vessels of the Old World species of *Ephedra* appear as a pair of bands flanking a pit aperture. Less conspicuous bands of this sort are shown for *E. przewalskii* in Figure 26; more pronounced thickenings are illustrated for the same species in Figure 27. Instances like this, or even more pronounced, as in Figure 28, where the bands extend around the vessel element, are designated by "++" in Table 1, column 12. The more pronounced thickenings in vessels have a helical orientation on the vessel wall.

The more pronounced thickenings on vessel walls of Old World species of *Ephedra* do not form the high relief reported for vessels of the New World species (Carlquist 1989). Relatively pronounced vessel wall thickening is reported here only for six species; helical sculpture on vessel walls has not hitherto been reported for Old World species of *Ephedra*.

Thickenings in tracheids of Old World species are less common than thickenings in the tracheids of New World species of *Ephedra*. Thickenings were observed only in tracheids of *E. distachya* var. *monostachya* (Fig. 29), *E. gerardiana*, *Polunin 884* (Fig. 30), and *E. monosperma*. The thickenings in tracheids form sharply ascending helical patterns. The three species in which helical thickenings are reported in tracheids occur in very extreme climatic conditions. In the New World species of *Ephedra*, helical thickenings are present in tracheids in all species that have thickenings in vessels. The ecological significance of helical thickenings in vessels will be explored in the conclusions section of this paper.

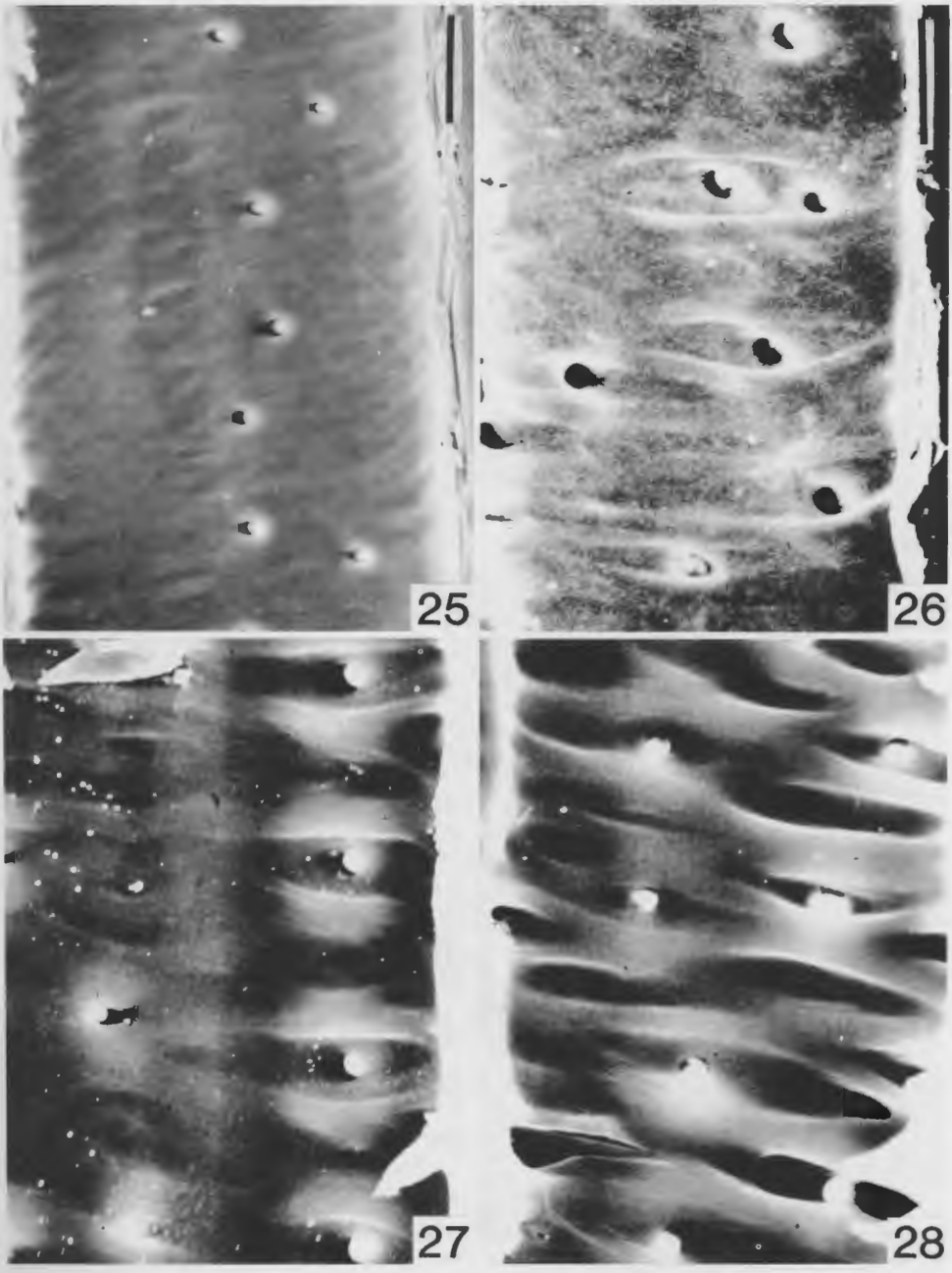

Fig. 25–28. SEM photographs of vessel walls of *Ephedra* from radial sections, to show wall sculpture.—25. *E. equisetina* (*Elias 9840*), sculpture composed of inconspicuous relief.—26–28. *E. przewalskii* (*Morefield 4991*).—26. Low relief, composed of thickenings paired beside pits.—27. Higher relief, composed of thickenings paired beside pits.—28. Higher relief, thickenings continue around vessel. (Fig. 25, scale at upper right in Fig. 25 [bar = 10 μm]; Fig. 26–28, scale at upper right in Fig. 26 [bar = 10 μm].)

Helical splits, leading away from pits, were observed in vessels and tracheids of *E. gerardiana* (*Polunin 884*). This is an indication of gelatinous wall composition rather than helical sculpture.

Axial Parenchyma

Cells similar to fiber-tracheids but subdivided horizontally into a pair of cells, each surrounded by a lignified wall, were observed quite infrequently in the Old World species of *Ephedra,* contrary to the report of Fahn et al. (1986), who claim "few celled strands" for all four of the species they studied. A transverse wall, indicating a two-celled strand of parenchyma, is illustrated here for *E. kokanica* (Fig. 31). Such strands were also observed in appreciable numbers in *E. foliata*; in no species are these strands common.

Rays

Ray histology is illustrated in Figure 33–41. Ray features are also summarized in Table 1. Column 13 gives height of uniseriate rays. Figures are omitted in that column if only a very few uniseriate rays were present in a section. Certainly in all species, multiseriate rays are more common than uniseriate rays. Uniseriate rays are relatively common in *E. kokanica* (Fig. 33), *E. aphylla, E. foliata,* and *E. fragilis.* Uniseriate rays are rather short: the mean for the Old World species in which they were measured is 190 μm. Uniseriate rays are relatively uniform in height, and do not fluctuate greatly from species to species. In these respects, they agree with uniseriate rays of the New World species.

Multiseriate ray height is given in Table 1, column 14. In contrast with uniseriate rays, multiseriate rays for the Old World species as a whole average 1326 μm. If vessel elements reflect fusiform cambial initial length in *Ephedra* as they do in dicotyledons, uniseriate ray height is much shorter than fusiform cambial initial length, whereas multiseriate ray height averages twice as tall. Thus, origin of uniseriate rays by subdivision of fusiform cambial initials into a series of ray initials seems unlikely. There appears to be no relationship between multiseriate ray height and diameter of sample. Tall multiseriate rays may be found both in large diameter samples (*E. altissima*) and small ones (*E. fragilis, E. pachyclada*).

Multiseriate ray width is given in terms of numbers of cells at the widest point in Table 1, column 15. Relatively few rays are biseriate, a fact that may relate to the paucity of uniseriate rays. The typical width of multiseriate rays (which averages 4.1 cells at the widest point in Old World species) is shown in Figure 34, 35, and 37.

Ray cells in *Ephedra* often appear rhomboidal rather than rectangular as seen in transections of wood (Fig. 36–38) or radial sections (Fig. 39, 40). The reason for this, explained in an earlier paper (Carlquist 1989), is that the cambium does not add equally to all fascicular xylem segments (axial portions between any two multiseriate rays as seen in transection). For example, one can see a marked offset between where the growth ring ends in the left side on Figure 36 and the right side. The ray cells are angled so as to interconnect equivalent places in the growth ring in these segments. The effect can be studied more closely in the higher magnification photograph of Figure 38, where the ray cell walls run quite obliquely rather than tangentially and radially. Where rays have such oblique cells, and where two rays fuse into one, as in Figure 37, center, a "herringbone" pattern is

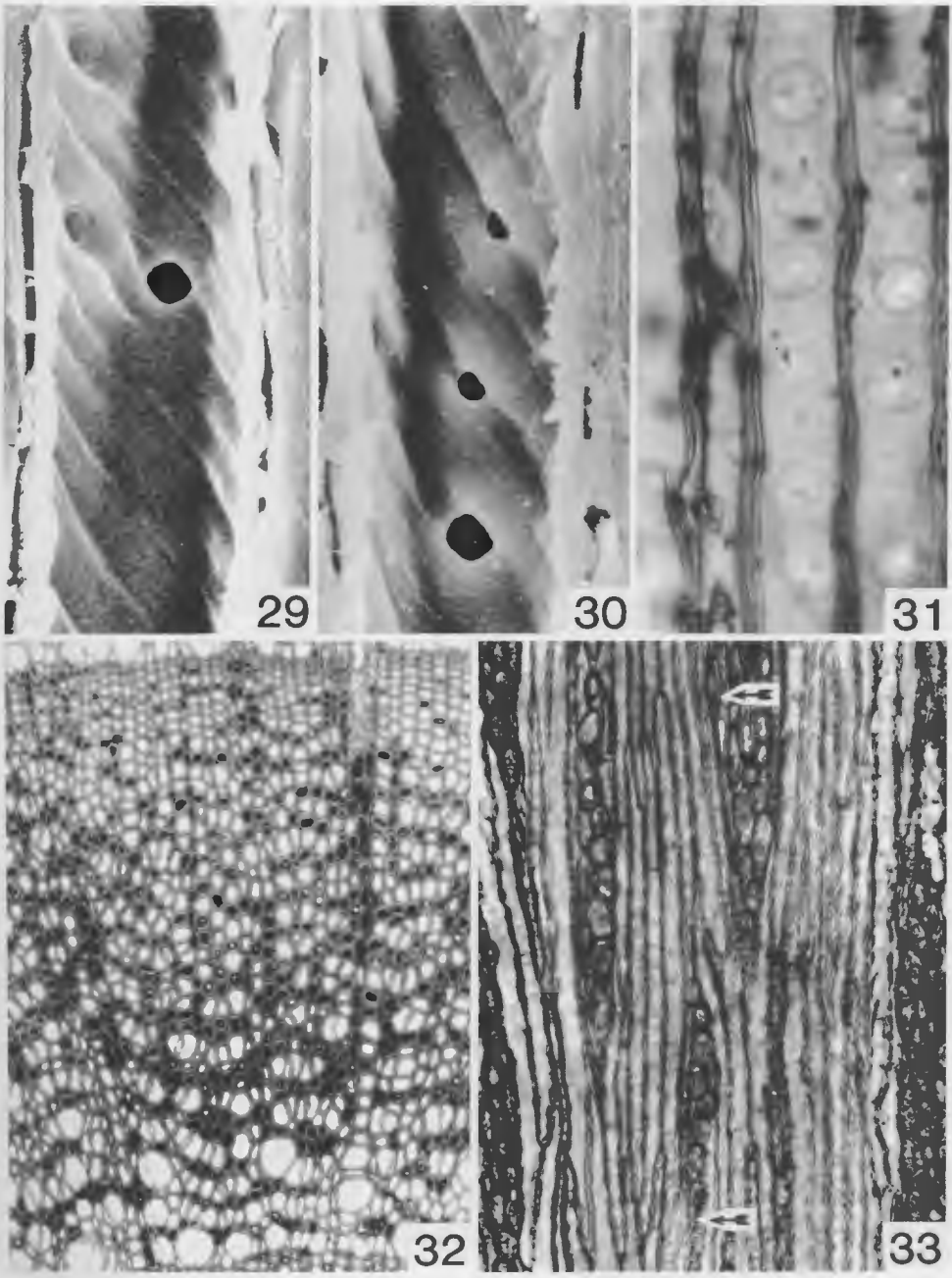

Fig. 29–33. Wood sections of *Ephedra*—29–30. SEM photographs of inner surfaces of tracheids from radial sections showing helical sculpture.—29. *E. distachya* var. *monostachya* (*Cambridge University Botanic Garden*), thickenings prominent on all wall portions.—30. *E. gerardiana* (*Polunin 884*), thickenings most prominent in vicinity of pits.—31. *E. kokanica* (*Hortus Botanicus Nikitensis*), radial section, showing two tracheids (left) and two axial parenchyma cells separated by wall (right).—32. *E. equisetina* (*Elias 9746*), transection, showing one growth ring; cells with dark contents are fiber-tracheids.—33. *E. kokanica* (*Hortus Botanicus Nikitensis*), tangential section to close approach to storied condition; arrows indicate levels at which tracheids terminate. (Fig. 29, 30, scale in Fig. 20; Fig. 31, scale above Fig. 24; Fig. 33, scale about Fig. 2.)

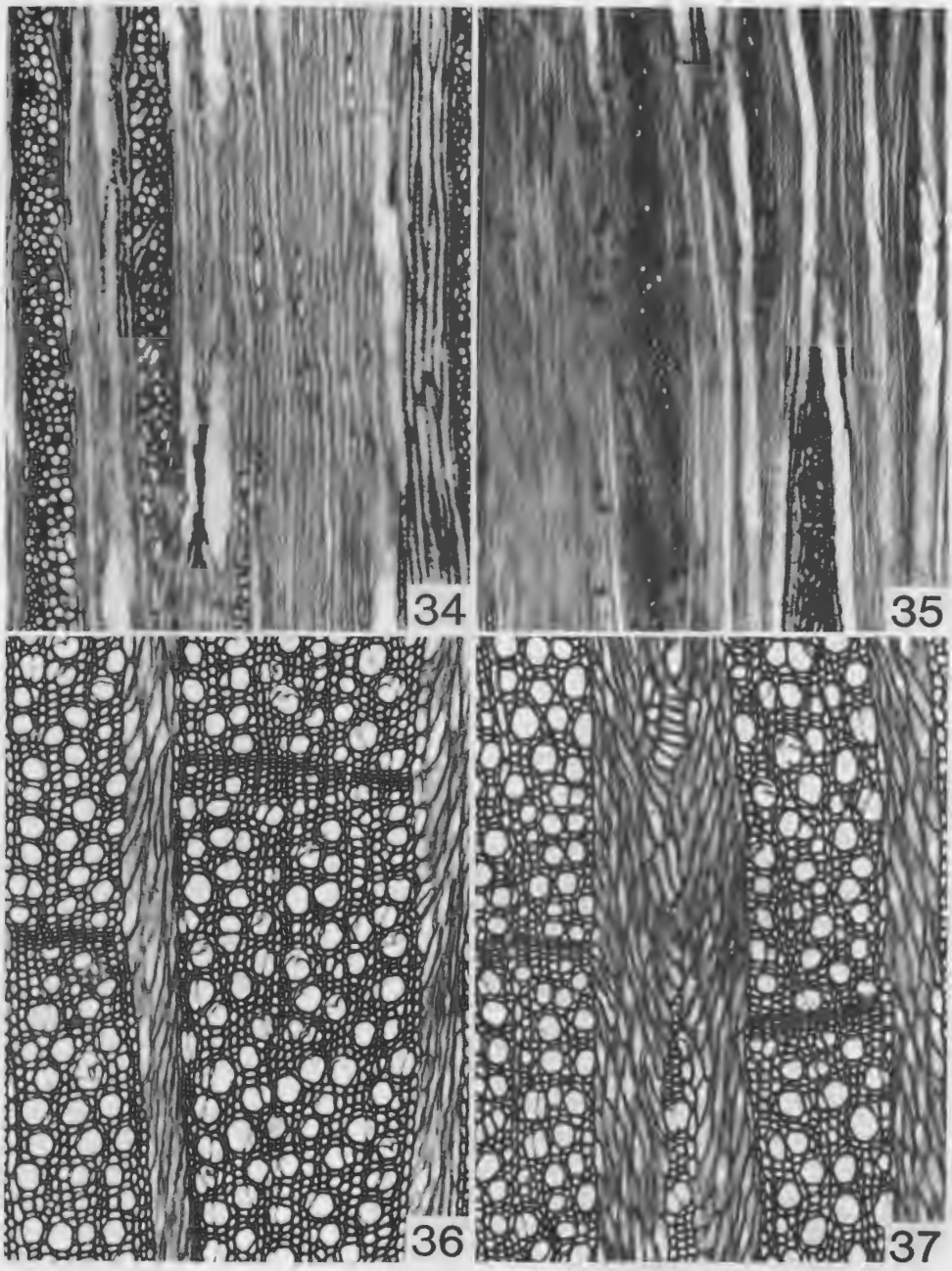

Fig. 34–37. Sections of *Ephedra* wood to show details of rays.—34. *E. aphylla* (*SJRw-12724*), tangential section to show uniseriate rays (right half of photograph).—35. *E. przewalskii* (*Morefield 4991*), tangential section; all rays are multiseriate.—36–37. *E. altissima* (*SJRw-12725*), transections to show angled ray cells related to offsetting in wood segments.—36. Offset between left (growth ring ends at middle of photograph) and right (growth ring ends further up).—37. Two rays (below, middle) fuse into one (above, middle); angled ray cells in opposing directions comprise ray above, middle. (Fig. 34–37, scale at top of Fig. 1.)

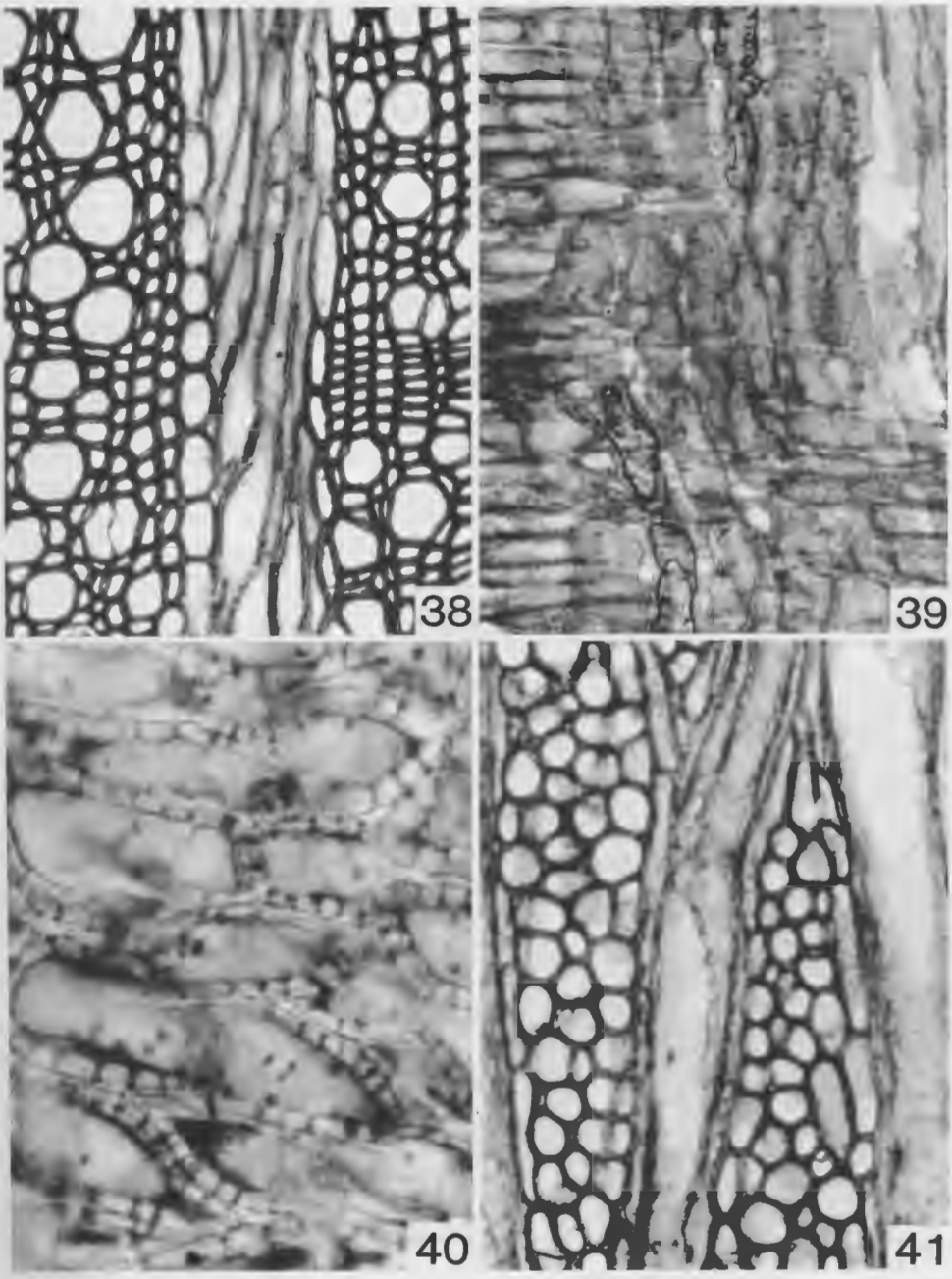

Fig. 38–41. Details of rays of *Ephedra*.—38. *E. altissima* (*SJRw-12725*), transection, ray cell walls are strongly oblique in orientation.—39. *E. aphylla* (*SJRw-12724*), radial section showing air spaces among the ray cells ("disjunctive ray cells"), especially in center, top to bottom.—40. *E. sinica* (*Liston 835-8*), ray cells from radial section, showing borders on pits between cells.—41. *E. fragilis* (*Palermo Botanic Garden*), tangential section showing upright ray cells sheathing most surfaces of the multiseriate rays. (Fig. 38, 39, 41, scale above Fig. 2; Fig. 40, scale above Fig. 24.)

achieved: oblique cells in opposed directions in the combined ray. The majority of Old World species showed ray cells with rhomboidal shapes, corresponding to offsets in fascicular xylem segments.

Although a ray fusion is illustrated in Figure 37, ray fusions appear uncommon in *Ephedra*. Events of ray breakup also are uncommon. I would not identify any grouped multiseriate rays I have seen in *Ephedra* as compound rays. Fahn et al. (1986) report compound rays for *E. alata*.

Ray cell wall thickness is reported in Table 1, column 16. Most species deviate only a little from the mean wall thickness for the species studied here, 2.7 μm. Notably thick ray cell walls were observed in *E. procera* and *E. przewalskii* (Fig. 35). Thin-walled nonlignified ray cells characterize the stems of *E. gerardiana, Ludlow 4074* (note notch at tops of photographs, Figures 12 and 13, denoting collapsed ray cells). The stems of *E. monosperma* also have thin-walled nonlignified cells, evident in the spaces between fascicular areas in Figure 7, where ray cells have collapsed. In both *E. gerardiana, Ludlow 4074,* and *E. monosperma,* upright stems buried by sand or below ground level provided the wood samples; this seems related to the nature of the ray cell walls.

Histology of multiseriate rays is summarized in Table 1, column 17. Uniseriate ray cells thoughout the species studied are mostly upright, with a few square cells. Multiseriate rays conform to a similar pattern in *E. alata, E. campylopoda, E. distachya* var. *monostachya, E. gerardiana* (*Freitag 1425*), *E. kokanica, E. lomatolepis, E. pachyclada* and *E. sarcocarpa.* If one compares this roster to sample diameter (Table 1, column 1), one finds that the samples with predominantly upright ray cells plus only a few square cells occur only in samples 5 mm or less in diameter, and that all samples in the smaller size class have this ray histology. Because more samples of small diameter were used in the present study than in the earlier one (Carlquist 1989), the present study demonstrates the relationship between sample diameter and ray histology definitively (Table 2).

Procumbent ray cells are present in multiseriate rays of specimens with large sample diameter (Table 1, column 17). Procumbent ray cells tend to occupy the central regions of multiseriate rays (Fig. 39, 41). Upright ray cells are present as sheathing cells on multiseriate rays (Fig. 41), in agreement with the descriptions given for wood of four *Ephedra* species by Fahn et al. (1986). Uniseriate wings on multiseriate rays are infrequent.

A few cells in multiseriate rays are disjunctive: conspicuous air spaces form between them (Fig. 39). These spaces mostly form separations in tangential walls rather than vertical radial and horizontal ray cell walls.

Ray cell walls bear pits that are often conspicuously or inconspicuously bordered as seen in sectional view (Fig. 40). Bordered pits were recorded as abundant in ray cell walls except in the samples that had ray cell walls with thin unlignified

Table 2. Sample diameter compared to quantitative wood features.

Sample diameter, mm	Mean no. of vessels per mm²	Mean vessel diameter, μm	Mean vessel element length, μm	Mean tracheid length, μm
>10 (N = 11)	92	38	753	789
<6 (N = 11)	93	31	589	696

walls (*E. gerardiana, E. monosperma*). Bordered pits on ray cells were also reported in the New World species (Carlquist 1989). Bordered pits in *Ephedra* ray cells tend to be more common on tangentially oriented walls, but as shown in Figure 40, bordered pits are often just as common on walls oriented in other directions. Attention is called to the fact that one can see borders on ray cell pits clearly only in sectional view. Radial sections are ideal for seeing these pits in sectional view. Lack of reports of bordered pits in ray cell walls is probably due to the difficulty of seeing borders on ray cell pits in alternative ways. Borders are not mentioned on ray cell pits by Fahn et al. (1986), who claim that vessel-to-ray pits are half bordered (simple pits on the ray side of the contact). Careful search has revealed only fully bordered pit pairs in vessel-to-ray pits in my material. However, I should stress that contacts between vessels and ray cells are infrequent, although contacts between tracheids and ray cells are common (see for example Fig. 38). The concept of vessel restriction patterns (Carlquist and Zona 1988) is probably not truly applicable to this paucity of vessel-ray contacts, but certainly one notices fewer vessels in contact with rays than one would expect on the basis of random vessel distribution.

Storied Structure

In the New World species of *Ephedra,* a nearly storied condition was reported in only one species, although some tendency could be observed in other species (Carlquist 1988). This tendency can also be seen in some of the Old World species. In the stem of *E. kokanica, cult. Hortu. Bot. Nikitensis* (Fig. 33), tracheids tend to terminate at particular levels (indicated by arrows). These levels are not so neatly demarcated as in angiosperms with short imperforate tracheary elements (usually libriform fibers), but the phenomenon is nevertheless a real one. A tendency toward storied structure was also observed in *E. equisetina* (*Elias 9746*) and *E. foliata.* Together with the previous report of storying in the genus, the present account confirms *Ephedra* as the first genus of gymnosperms in which storying, or a tendency toward it, has been reported. Storying is related to shortness of the fusiform cambial initials (Bailey 1923), so the occurrence of storying in *Ephedra* rather than in any other gymnosperm is to be expected. The tracheids of *Ephedra* are shorter than those of other gymnosperms (Bailey and Tupper 1918).

One hint of the storied condition can be seen in a transection of *E. equisetina* (Fig. 24). The tracheids in that transection all appear at approximately their widest diameter. If storying were absent, one would expect narrow tracheid tips to be intermixed at random with wider segments of tracheids in a transection.

Crystals

As in the New World species of *Ephedra,* minute rhomboidal calcium oxalate crystals occur on the surfaces of tracheary elements and wood ray cells in the specimens of the present study. These crystals are relatively sparser among tracheary elements (Fig. 43) than among ray cells (Fig. 42). The crystals are smaller on the surfaces of wood cells (Fig. 42, 43) than on the surfaces of phloem ray cells, where they are denser and show a great range in size (Fig. 44). At points where cells are closely appressed to each other, there are few crystals; they tend

to occur in the interstices among cells, lining intercellular spaces or filling what would otherwise be intercellular spaces (Fig. 42). Scanning electron microscopy confirms that crystals are not formed inside cell walls of *Ephedra,* but on surfaces of these cells. They may be somewhat embedded in the outer cell surfaces, but not deeply (Fig. 43). Crystals dislodged by the sectioning process may leave hexagonal impressions in the cell wall surface (Fig. 43). In the epidermis of *Ephedra,* crystals occur abundantly (Fig. 45), but apparently in the cuticle rather than in the epidermal cell wall, in agreement with the developmental findings of Oladele (1982), who worked with conifers.

Crystals were observed to be quite abundant in the wood of *E. campylopoda, E. ciliata* (*Grant 15309*), *E. distachya* var. *distachya, E. equisetina* (Fig. 43), *E. fragilis, E. intermedia,* and *E. przewalskii* (Fig. 42). Crystals were least abundant in the wood of *E. aphylla, E. ciliata* (*Koelz 13087*: crystals not seen upon careful search), *E. kokanica* (both collections), and *E. procera* (*Mulkidzhanyam 27-IX-1962*). The listings in the two preceding sentences are based mostly upon light microscopy. With light microscopy, crystals can readily be seen as a granular deposit among cells, but where scarce, they might be missed. Fahn et al. (1986) report crystals as absent from woods of the four *Ephedra* species they examined. Presumably they were looking for crystals inside cells rather than on the outer cell surfaces.

Cellular Contents

Starch was observed in ray cells of *E. alata, E. altissima, E. distachya* var. *distachya, E. foliata, E. fragilis, E. intermedia, E. kokanica,* and *E. procera.* Very likely, starch occurs widely in ray cells of the Old World species of *Ephedra,* but the dried specimens available are probably not uniformly suited to revealing the presence of starch. Starch occurrence was better demonstrated in the New World species (Carlquist 1989), in which more numerous specimens were available in liquid preserved form.

Massive deposits of darkly staining compounds are illustrated in the fiber-tracheids of *E. equisetina* (Fig. 32) and in the ray cells of *E. aphylla* (Fig. 39). Massive darkly staining deposits were also observed in ray cells of *E. aphylla* and *E. intermedia,* but droplets of these compounds can be observed in woods of many *Ephedra* species.

ANATOMICAL DESCRIPTIONS: BARK ANATOMY

Because bark is often attached to wood sections, observations on bark anatomy could be made conveniently. Because bark portions were not present on all samples provided, and adherence of bark to wood sections varied, comparable data are not available for all species. However, the range of phenomena seen in *Ephedra* bark is certainly evident.

As with the New World species of *Ephedra,* four types of sclerenchyma are present in the secondary phloem and periderm:

1. Fibers with gelatinous walls in the axial phloem.
2. Fibers with lignified walls in the axial phloem.

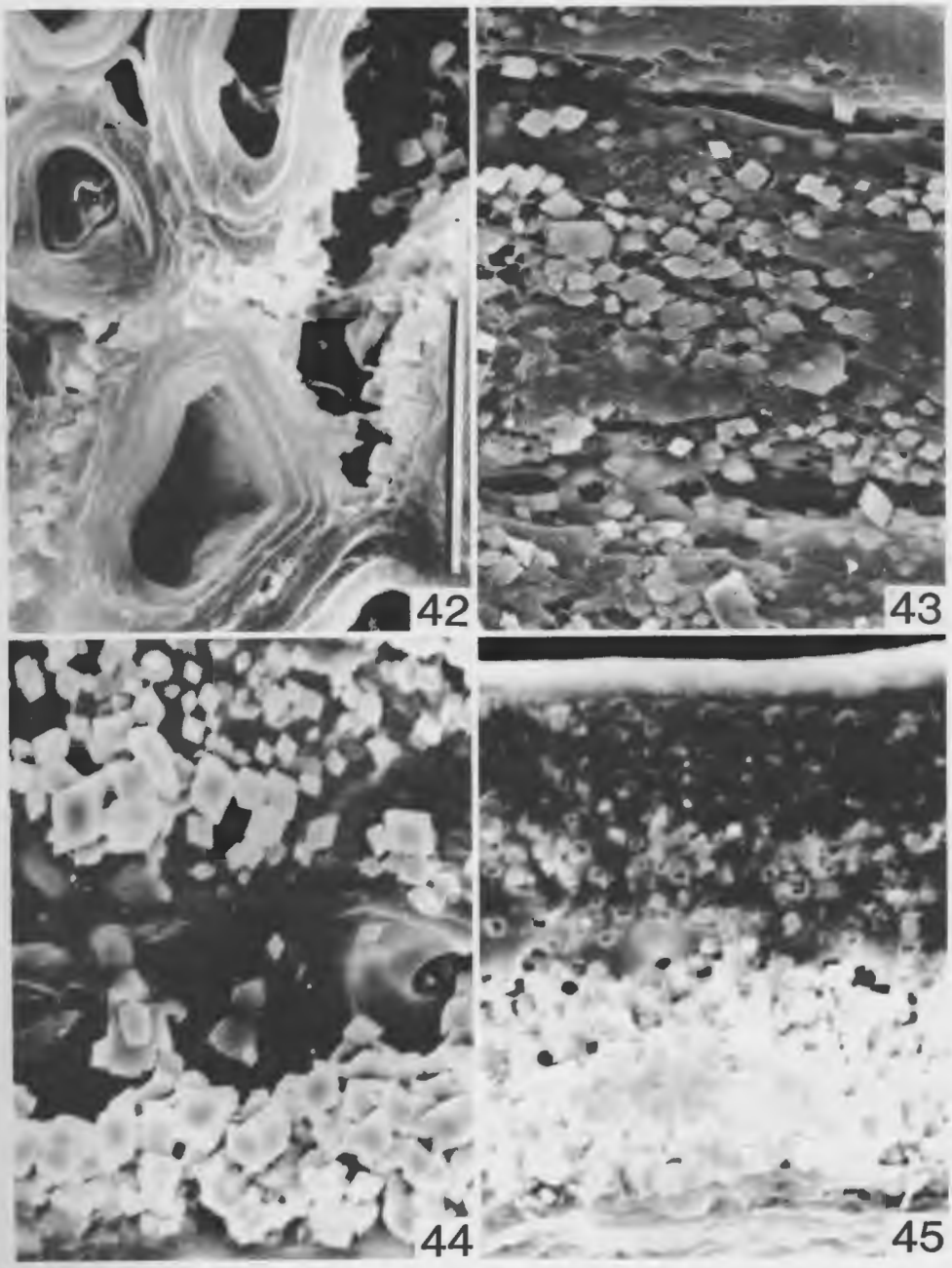

Fig. 42–45. SEM photographs of minute calcium oxalate crystals in stems of *Ephedra*.—42. *E. przewalskii* (*Morefield 4991*), ray cells from tangential section; crystals among ray cells.—43. *E. equisetina* (*Elias 9746*), crystals on tracheids from tangential section.—44–45. *E. pachyclada* (*Freitag 3424*), portions from stem radial section.—44. Crystals on outer surfaces of secondary phloem ray cells.—45. Outer wall of epidermal cell; most of the photograph (except for narrow strip at bottom) is cuticle (or cutinized wall), in which numerous crystals are embedded. (Fig. 43–45, scale at right in Fig. 42 [bar = 10 μm].)

3. Sclereids in phloem rays, formed from ray parenchyma.
4. Phelloderm sclereids.

There are species of *Ephedra* in which gelatinous fibers were not observed in bark. Absence of fibers is shown for *E. equisetina* in Figure 46. Only a short distance outside the cambium in Figure 46, sieve cells are crushed. Phloem parenchyma cells intermixed with the sieve cells enlarge and fill the space left by the shrivelling sieve cells. At the upper end of Figure 46 is a periderm. The phellogen has produced numerous layers of phellem, plus a few layers of thin-walled phelloderm. Species in which fibers with gelatinous walls were not observed in secondary phloem include *E. gerardiana* (*Ludlow 4074*) and *E. intermedia.*

Fibers with gelatinous walls, but without accompanying lignified fibers or sclereids with lignified walls, were observed in *E. aphylla* (*SJRw-12725*), *E. ciliata, E. distachya* var. *monostachya, E. equisetina, E. foliata* (Fig. 48, top), *E. fragilis, E. gerardiana* (*Freitag 1425, Polunin 884*), and *E. sarcocarpa.*

Fibers with gelatinous walls mixed with fibers with lignified walls are shown in Figure 47. The fibers with gelatinous walls, yellowish in unstained sections, stain dark red with safranin. This accounts for the very dark appearance of these fibers in Figure 47. The fibers with lignified walls were observed in bark of *E. alata, E. aphylla* (*Cambridge University Botanic Garden*), *E. campylopoda, E. distachya* var. *distachya, E. intermedia, E. kokanica, E. lomatolepis, E. major, E. procera, E. sarcocarpa* (Fig. 50, bottom; see enlarged, Fig. 52), and *E. sinica.*

Sclereids in ray areas are illustrated for *E. aphylla* in Figure 49 (below, middle). Other species in which ray sclereids were observed include *E. campylopoda, E. kokanica, E. major,* and *E. procera.*

Phellem consists of thin-walled cells that stain reddish with safranin (Fig. 49, above). Phellem cells are compacted at the outer surface of periderm, as shown in Figure 54 (right). Phelloderm, however, can consist of sclereids with lignified walls, as mentioned earlier (Carlquist 1989). Phelloderm sclereids are shown in Figure 48, just below center. Phelloderm sclereids may form as many as five layers per periderm. Phelloderm sclereids were observed in *E. foliata* and *E. kokanica,* which are closely related (if not actually conspecific). Very likely phelloderm sclereids characterize more of the Old World species than these, but sectioning of stems by means of a sliding microtome is likely to result in tearing the periderm away from bark, especially if it contains sclereids.

Phelloderm that is thin walled but rich in rhomboidal crystals of various sizes is illustrated here for *E. sarcocarpa.* Figure 50 shows the entire periderm together with underlying phloem that consists at this point mostly of fibers. In Figure 51, most of the photograph is devoted to the thin-walled phelloderm cells (phellem at top of photograph only). Crystals of various sizes, some much larger than those seen among xylem cells, densely cover the outside surfaces of the radially elongate phelloderm cells. In Figure 52, an enlarged portion of the juncture between crystalliferous phelloderm (above) and phloem fibers (below) is shown. The density of the crystals is evident. One can also see crystals among some of the outer fibers. Most of the fibers (those that appear pale gray) have lignified walls. A few fibers with gelatinous walls (darker gray) may also be seen. Crystals in thin-walled phelloderm are also illustrated for *E. procera* by means of SEM in Figure 54.

Successive periderms were not illustrated in the earlier study (Carlquist 1989),

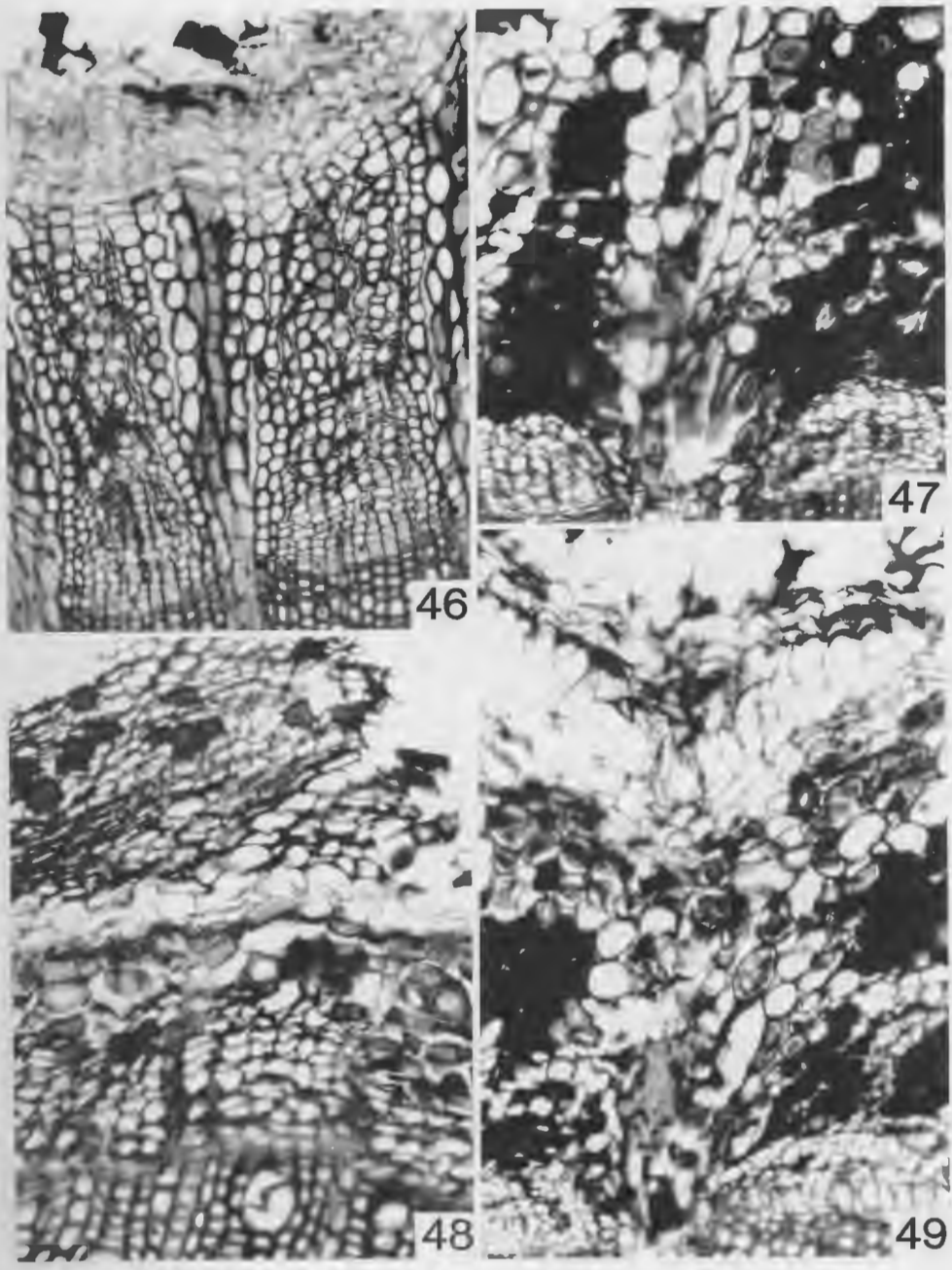

Fig. 46–49. Transections of bark of *Ephedra*.—46. *E. equisetina* (*Elias 9746*), periderm at top, secondary xylem at bottom; most of photograph shows secondary phloem devoid of fibers.—47. *E. aphylla* (*Cambridge University Botanic Garden*), secondary phloem rich in gelatinous fibers (dark); a few lignified fibers (upper right) also present.—48. *E. foliata* (*SJRw-37203*), gelatinous fibers in old secondary phloem (above), phelloderm sclereids (middle, left to right).—49. *E. aphylla* (*Cambridge University Botanic Garden*), bark with phellem above (pale cells), ray sclereids in phloem ray area, below, just left of center. (Fig. 46–49, scale above Fig. 2.)

although they may occur in all *Ephedra* species. Successive periderms are illustrated here for *E. campylopoda* (Fig. 53). The pale gray bands in that photograph are phellem; the darker strips represent collapse of secondary phloem.

ANATOMICAL OBSERVATIONS: PITH

Pith although not produced by secondary growth, is conveniently studied in stems sectioned on a sliding microtome. Comparative anatomy of pith has been very little studied in *Ephedra* (see Thompson 1912, Martens 1971), so an account is offered here.

Pith composed of thin-walled cells, but no sclereids and no fibers, was observed in *E. major, E. monosperma,* and *E. procera.*

The most common pith condition, both in New World and Old World species of *Ephedra,* consists of gelatinous fibers at the periphery of the pith, combined with thin-walled pith cells. A few such gelatinous fibers can be seen in Figure 57, top. Other species in which gelatinous fibers occur at the periphery of the pith include *E. aphylla, E. campylopoda, E. gerardiana* (*Freitag 1425*), *E. kokanica,* and *E. lomatolepis.*

In a few species gelatinous fibers were observed in strands throughout the pith. Sclereids can be found scattered throughout the pith. Both of these conditions were present in *E. sarcocarpa* (Fig. 55) and *E. alata* (Fig. 56). The great similarity between these species with respect to pith anatomy is interesting, because they are placed in divergent parts of the genus in Stapf's (1889) system. *Ephedra alata* belongs in Section *Alatae* (bracts of female strobili papery at maturity), whereas *E. sarcocarpa* is placed in Section *Ephedra* [= *Pseudobaccatae*] (bracts fleshy at maturity).

In a scattering of *Ephedra* species, dark deposits are present in pith cells. These may be seen in the pith of *E. distachya* var. *distachya.*

CONCLUSIONS

Wood Anatomy and Habit

In the earlier study (Carlquist 1989), correlations between wood anatomy and habit could be derived clearly: many samples studied were close to optimal size. This permitted one to separate differences that relate to habit or to ecology from those that represent degrees of juvenilism. More significantly, the New World species can be categorized rather easily with respect to habit. In the Old World shrubs, intermediate sizes between small and large occur, but, more significantly, in a number of species sprawling shrubs grade into climbing shrubs or even upright shrubs. In the Old World species, one can perhaps best categorize the effect of habit on wood anatomy by selecting particular species with distinctive habit features and comparing them to the earlier (Carlquist 1989) findings.

The medium-sized shrubs in the study of the New World *Ephedra* species showed values for mean total perforation area per mm^2 of transection of about 0.10. This value is also closely approximated here by the species *E. alata, E. distachya* var. *distachya, E. fragilis, E. intermedia, E. major, E. procera, E. przewalskii, E. sinaica,* and *E. strobilacea.* One of these, *E. fragilis,* can be described as having a scrambling habit, but it is not scandent. Species that could be termed scandent or ascending (values in parentheses from Table 1, column 10) include

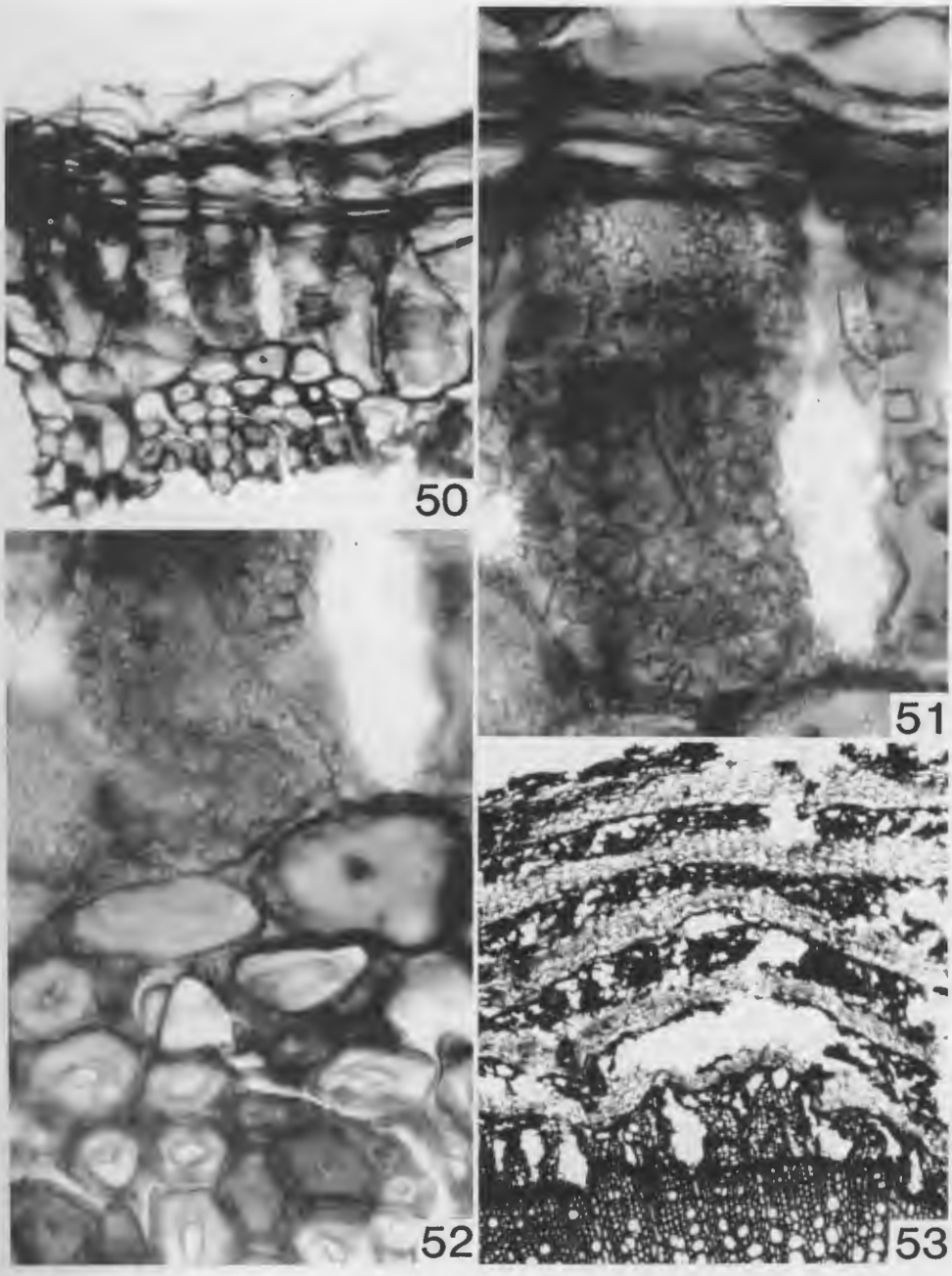

Fig. 50–53. Transections of bark of *Ephedra*.—50–52. *E. sarcocarpa* (*Freitag 14017*).—50. Portion of thin bark with periderm above, a few secondary phloem fibers below.—51. Portion of periderm to show phellem (flattened cells above), phelloderm cells (bottom three-quarters of photograph) densely bearing crystals.—52. Portion of crystal-bearing phelloderm (above) and fibers of secondary phloem (below).—53. *E. campylopoda* (*Davis 18067*), successive periderms; phellem bands pale gray, secondary phloem bands dark. (Fig. 50, scale above Fig. 2; Fig. 51, 52, scale above Fig. 24; Fig. 53, scale above Fig. 1.)

E. altissima (0.24), *E. aphylla* (0.30), *E. foliata* (0.36), and *E. kokanica* (0.24). These values are comparable to ones reported for the scandent species *E. pedunculata, E. triandra,* and *E. tweediana* (Carlquist 1989). *Ephedra equisetina* (0.12, 0.18, 0.14) has values above those of the other shrubs, perhaps because it is a large shrub rather than a small one; treelike shrubs in the earlier study had values above 0.10.

The very low perforation area values for *E. gerardiana* (0.04, 0.0006, 0.01) and *E. monosperma* (0.006) relate to their entry into a nearly vesselless condition, rather than diminution in size by itself, and ecology is inseparably related to habit for these two species. Values lower than one would expect for shrubs (e.g., *E. campylopoda,* 0.05) are probably related to diameter of the wood sample. If one takes a twig sample from a large shrub, one obtains wood the quantitative features of which are like those of a small shrub. For example, in angiosperms, wood of branches has narrower vessels and more numerous vessels per mm^2 than one finds in the main stem (Carlquist 1969). The value for combined area of perforations per mm^2 was similar for scandent species and treelike species of *Ephedra* in the earlier study (Carlquist 1989). The relatively high value for *E. aphylla* might correspond to either habit, because the habit of this species, according to Stapf (1889), can be either a climbing or a self-supporting large shrub.

Growth rings of scandent and sprawling species are of type 1 (vessels only slightly narrower in latewood, not fewer in number than in earlywood). This is in accord with the relatively greater area of stems devoted to conduction in scandent dicotyledons, as compared to nonscandent ones (Carlquist 1975). The larger area devoted to conduction is evident also in the total perforation area per mm^2 for *Ephedra.* This may, in turn, be an expression of the greater transpirational requirements of larger shrubs as compared to smaller ones, because scandent *Ephedra* species tend to be large and bear more total transpirational stem area than do nonscandent shrubby species of *Ephedra.* Larger scandent *Ephedra* species do not grow in localities extreme for the genus, so that the loss of safety that is inevitably coupled with greater transection area devoted to conduction is tolerable.

Wood Anatomy and Organography

Because I was unable to collect wood samples of Old World species of *Ephedra,* samples from various parts of a single plant were not available. Thereby, I could not compare wood of roots, upright stems, and underground stems. Such comparisons were made for wood of the New World species (Carlquist 1989). Wood of roots proved to be more mesomorphic (e.g., wider vessels) than that of stems; wood of underground stems was intermediate. Greater width of rays—perhaps related to storage of water and starch—was observed in roots as compared to stems. *Ephedra monosperma* forms a very diminutive shrub (less than 1 dm tall) according to Stapf (1889). Bobrov (1968) described it as having stems, apparently buried in the soil, arising from a knotty caudex. The habit of *E. gerardiana* (*Ludlow 4074*) is not dissimilar. The stems of this specimen were very short, perhaps the result of browsing, so the stem studied was apparently an underground stem from which the aerial stems branched. Both in *E. monosperma* and the collection of *E. gerardiana* just described, multiseriate rays are composed of thin-walled nonlignified cells. Lack of mechanical strength in these ray cells may be related to the

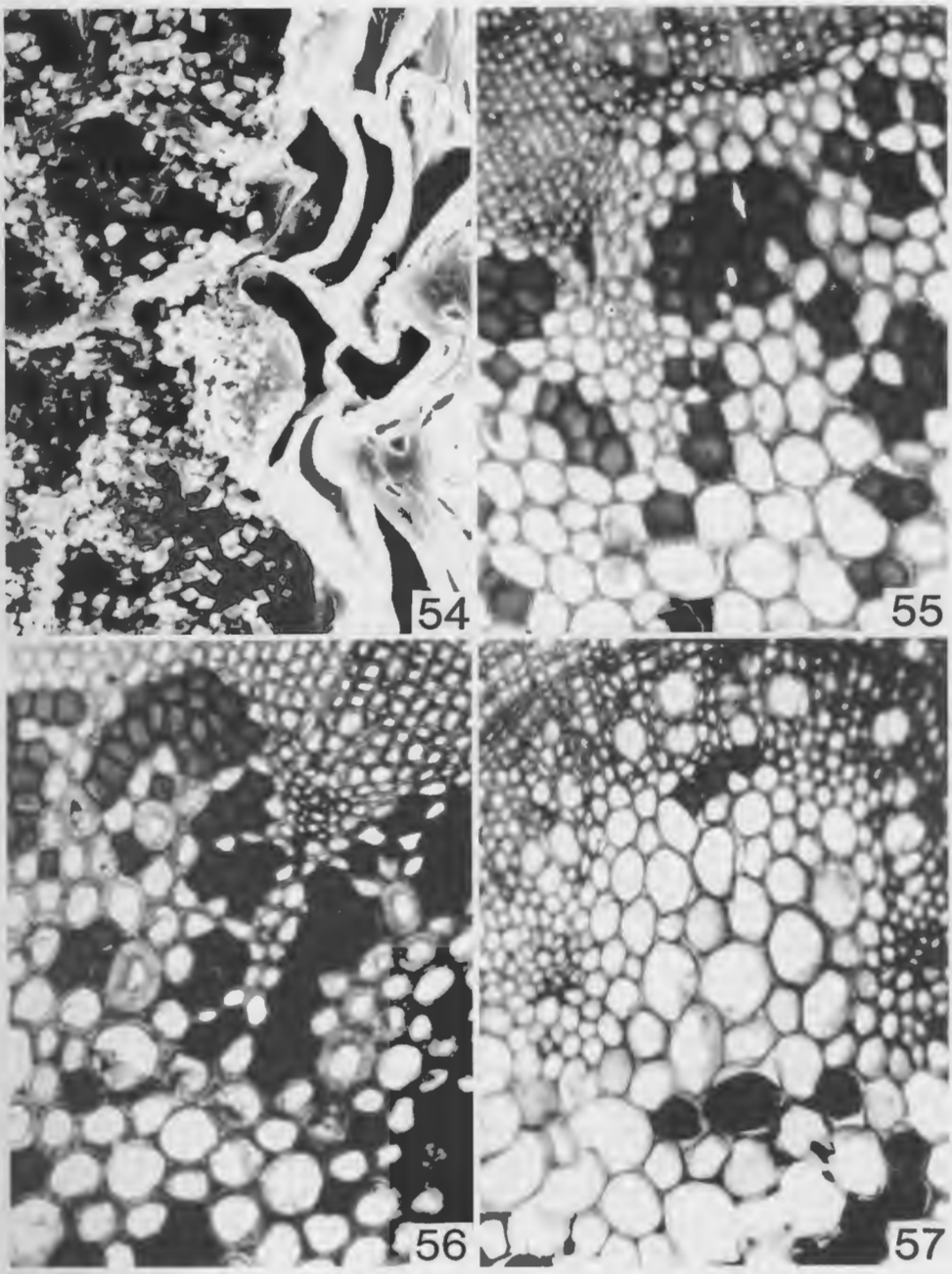

Fig. 54–57. Bark and pith features of *Ephedra*.—54. *E. procera* (*Mulkidzhanyam 27-IX-1962*), compressed phellem cells (right) and subadjacent crystalliferous phelloderm cells (left).—55–57. Transections of pith.—55. *E. sarcocarpa* (*Freitag 14017*), patches of gelatinous fibers (dark).—56. *E. alata* (*Harris 26-III-1960*), gelatinous fibers (dark) plus sclereids with variously thick walls and thin-walled pith cells.—57. *E. distachya* var. *distachya* (*Mulkidzhanyam 13-VII-1965*), a few gelatinous fibers at pith periphery (above) and (below), thin-walled cells with dark contents. (Fig. 54, scale in Fig. 25; Fig. 55–57, scale above Fig. 2.)

underground nature of the stems. Also, nonlignified cells with thin walls would readily accommodate changes in volume if storage of water within the stem fluctuated with season.

If thick lignified ray cell walls contribute to mechanical strength of a shrub, one would expect them in larger shrubs. The Old World species of *Ephedra* with ray cell wall thickness greater than 3.0 μm include *E. altissima, E. equisetina, E. procera,* and *E. przewalskii* (Table 1, column 16). All of these species are shrubs more than 1 m tall according to Stapf (1889) and Bobrov (1968); the sample diameter was also of greater than twig size for these species.

Wood Anatomy and Ontogeny

A clear trend showing increase in vessel element length or tracheid length with increase in stem diameter was demonstrated in the New World species of *Ephedra* (Carlquist 1989). Likewise, that study showed increase in vessel diameter with stem diameter. Comparable data are obtainable from the present study (Table 2).

One would expect that if vessel diameter increases with sample diameter, vessel density ought to decrease. That result is not obtained from figures represented in Table 2, yet I believe the data are representative (e.g., one nearly vesselless specimen falls under each of the two specimen-diameter categories). The increase in vessel diameter shown in Table 2 certainly appears valid, judging from the New World species (Carlquist 1989, Table 1). Increase in vessel diameter with sample diameter is probably a common trend in dicotyledons, but is often not reported because sample diameter is usually unknown or unreported. Increased vessel diameter would have the effect of providing greater conductivity. The fact that vessel density stays the same suggests that conductive safety is not lessened. Perhaps conductive safety is theoretically lessened slightly, for if vessel density stays the same while vessel diameter increases, there would have to be a small diminution in number of tracheids per mm^2. Tracheids have the ability to confine air within individual cells, bounded as they are by membranes in pits; in vessels, bubbles can, at least theoretically, spread from one vessel element into an entire series of vessel elements. Therefore increased vessel area would lessen conductive safety, but I believe that tracheids are present in such large numbers in *Ephedra* wood that any of such diminution of conductive safety would be small.

Increase in length of vessel elements and tracheids with increase in sample diameter is clear, if not dramatic, as demonstrated in Table 2. This trend accords with the findings of Bailey and Tupper (1918) and subsequent research.

Also cited in the anatomical descriptions above, as well as in the study of the New World species, is the tendency for ray cells in small stems to be upright or square, whereas ray cells in larger stems are commonly to predominantly procumbent, with upright cells restricted to sheathing positions in multiseriate rays. Although not demonstrated with clarity in the present study, the New World Ephedras show widening and lengthening of multiseriate rays with increase in sample diameter to a significant degree (Carlquist 1989, Table 4).

Storying is reported in three species here (*E. equisetina, E. foliata, E. kokanica*). The wood samples of *E. kokanica* were not notably large in diameter, so degree of storying does not seem directly related to age. In dicotyledons, there is a tendency for less storying in twigs than in mature stems, but the onset of storying occurs relatively early (Bailey 1923). One would like to know if storying would

have been even more pronounced had samples of large diameter of *E. kokanica* been studied.

Wood and Bark Anatomy and Ecology

Determining the ecological regimes in which the various specimens grew is nearly impossible. One can, however, find ways of showing the relationship between ecology and wood anatomy in *Ephedra*. *Ephedra* localities range from dry to extremely dry, and from cool in winter to extremely cold. *Ephedra* on the steppes of Asia must experience extreme summer heat as well. High alpine species, from localities above 4000 m, such as *E. gerardiana* in Tibet and *E. rupestris* in Argentina, experience extremes of both cold and dryness. The high-alpine species may well experience a growing season of only a few weeks per year.

The occurrence of helical thickenings in vessels of *Ephedra* is interesting with relationship to ecology. In the New World species, this feature may be monophyletic; it characterizes only fleshy bracted North American species, and is absent in all South American species, regardless of habitat. In the Old World species, helical thickenings are not present in species centered in southern Europe, North Africa, Mediterranean islands and shores, and India. Helical sculpture is characteristic of species of Central Asia, from western China (*E. przewalskii, E. sinica*) to the Middle East (*E. distachya, E. sarcocarpa, E. strobilacea*). These species belong to section Alatae (*E. przewalskii*) as well as section *Ephedra* (*Pseudobaccatae*). Helical sculpture in vessels may have originated polyphyletically in the Old World species, and probably has originated independently of the phenomenon in the New World species (in which helical thickenings are present in tracheids of any species in which they are present in vessels, unlike the condition in the Old World species).

Certainly in dicotyledons there is a relationship between extreme climates, particularly those involving coldness or dryness, and presence of helical thickenings (e.g., Baas 1973; Carlquist 1966, 1982). The geographical distribution of the Old World species of *Ephedra* with helical thickenings in vessels or tracheids corresponds to areas with strongly continental climates, and extremes of coolness, heat, and drought. Let us assume, then, that helical thickenings in *Ephedra* are one indicator of climatic extremes. Table 3 has been constructed using helical thickenings in vessels in order to see what other features of wood may be indicative of xeromorphy.

In Table 3, vessel diameter is less in species with helical thickenings, as would be expected if narrow vessels are a criterion of xeromorphy. Narrowness of vessels is certainly an indicator of xeromorphy in woods of dicotyledons (Carlquist 1966, 1975). If one has in mind vessel density of xeromorphic dicotyledons (Carlquist 1966, 1975) and looks at the results in *Ephedra* (Table 3), however, one obtains

Table 3. Helical sculpture in tracheary elements compared to quantitative wood features.

Degree of sculpture presence	Mean number of vessels per mm^2	Mean vessel diamter, μm	Mean vessel element length, μm
Present (N = 14)	59	30	573
Absent (N = 21)	104	35	650

an unexpected result: vessels are fewer per mm^2 in species with helical thickenings than in those that lack them. In fact, the results in *Ephedra* are exactly what one would expect if one takes into account the conductive safety of tracheids: tracheids are safer than vessels according to the considerations mentioned earlier (see also Ewers 1985). All of the nearly vesselless Old World species of *Ephedra* have helical thickenings in vessels. The replacement of vessels by tracheids in the woods, so to speak, can be seen as a gain in conductive safety. One can, however, also interpret an approach to vessellessness in these species of *Ephedra* as lack of selection for the conductive efficiency that vessels might supply, a lack of selection quite understandable in these plants, which have such small size and, in relatively cold conditions, presumably low transpiration and conduction rates. In either case, reduction of vessel density in *Ephedra* can, as Table 3 indicates, represent xeromorphy.

Table 3 seems to show that species with helical thickenings also have shorter vessel elements than those without helical thickenings (tracheid length, not presented in this table, would show the same pattern). However, shorter vessel elements in these species may connote smaller plant size, which is correlated with shorter tracheary element length in conifers (Carlquist 1975).

Allied to reduction in vessel density identified in Table 3 as a xeromorphic trend is the absence of vessels in latewood of growth rings ("0" in Table 1, column 2). This strategy combines conductive efficiency of earlywood with optimal safety of latewood (or lack of requirement for conductive efficiency in latewood), as in the dicotyledonous type 5 growth rings (Carlquist 1980). This strategy is not available to dicotyledons that have fiber-tracheids or libriform fibers instead of tracheids.

The presence of minute calcium oxalate crystals on the surface of wood and bark cells was reported in the New World species (Carlquist 1989) and these crystals are equally prevalent in the Old World species, although crystals are more abundant in some species than in others. Crystals are larger and denser on surfaces of phloem and phelloderm cells than crystals on outer surfaces of xylem cells in *Ephedra*. Greater abundance and size of crystals in peripheral positions of the stem, lesser abundance and size of crystals in the wood correlate with deterrence of a chewing or boring insect. There has been little work demonstrating the effectiveness of crystals in this way, however, and one must concede data would be difficult to obtain. Likewise, there is a presumption, largely untested, that sclereids and fibers, such as one sees in bark and pith of *Ephedra*, also function in deterring predation by insects or larger animals.

One might think that wood anatomy of *Ephedra* would be readily altered by cultivation. Some features one might expect to show modification as a result of greater water availability in cultivation would be vessel diameter and nature of growth rings. The following species in the present paper are represented by both cultivated and wild-collected specimens: *E. altissima*, *E. aphylla*, and *E. procera*. In each of these pairs, there is little difference in vessel diameter between the cultivated and the wild-collected specimen. These pairs may provide an insufficient basis for interpretation. Alternatively, cultivation may not be as favorable as one may suspect. Even though botanic gardens do tend to have greater water availability than wild areas, botanic gardens may have colder winters. A large number of *Ephedra* species are cultivated at the Cambridge University Botanical

Garden and the Copenhagen Botanical Garden. Although these localities do not have truly continental winters in terms of extreme lows, winters in these cities are certainly harsher than in areas with Mediterranean-type climates, and *Ephedra* species from such climates are grown in these cities. That a large number of *Ephedra* species can be cultivated in these localities is, in fact, surprising.

Wood, Bark, and Pith Anatomy and Systematics

Very few wood features in *Ephedra* are distributed in a way that corresponds to the infrageneric classification of Stapf (1889), the best attempt to date at creating an infrageneric system for *Ephedra.*

The growth-ring types show considerable variability. However, the type 1 growth ring (latewood vessels very little narrower or less numerous than earlywood vessels) is evidently characteristic of particular species. Most of these are climbing species, so that one might credit Stapf's "tribe" *Scandentes* as a natural group on the basis of this single feature. However, *E. americana* H. & B., an upright shrub, also has growth rings of this type. In the case of this species, the relatively nonseasonal climate in the subtropical latitudes of the central Peruvian Andes, rather than a climbing habit, is correlated with the growth-ring type.

Ephedra americana consistently has borders on perforations to a rather more prominent degree than one finds in other species. Prominently bordered perforations may be found in occasional narrow vessels in other species. Helical thickenings in vessels and tracheids are not present in all of the species that occur in extreme environments. The genetic information that leads to formation of helical sculpture probably is not readily evolved, and thus this feature may be regarded as a specific criterion in the species that possess it.

A tendency toward storying of tracheids was noted in roots of *E. coryi* Reed var. *viscida* Cutler (Carlquist 1989); in the present study, it was observed in *E. equisetina, E. foliata,* and *E. kokanica.* This feature is not yet reliably enough established so that one can use it as a specific criterion, but further investigation of this feature is certainly warranted.

Presence of notably thick-walled ray cells in *E. equisetina, E. procera,* and *E. przewalskii* is a feature worthy of consideration as a specific criterion in those species. Presence of uniseriate rays in appreciable numbers (multiseriate rays occur in all species) is characteristic of *E. aphylla, E. foliata, E. intermedia,* and *E. kokanica* among the Old World species, and a scattering of New World species. Three of the species just listed are climbing species, but one is not; in the New World species, one species in which uniseriate rays are common is the climbing *E. pedunculata,* but two New World species with uniseriate rays are nonscandent. Both the ray cell wall thickness and the presence of uniseriate rays are, however, difficult to express in quantitative terms.

Occurrence of crystals in very small numbers (*E. pedunculata*) or large numbers (*E. przewalskii, E. trifurca*) may be of specific significance, although relative abundance is difficult to express in quantitative terms.

Very likely there are some specific criteria in bark and pith anatomy. The occurrence of strands of gelatinous fibers scattered throughout the pith, together with isolated thick-walled sclereids, was observed in *E. alata* and *E. sarcocarpa* but not in other species.

Even more difficult than establishment of specific criteria within the genus with respect to wood, bark, and pith anatomy is establishment of polarity in these character states. Are the relatively prominent borders on perforations, the presence of uniseriate rays, and the type 1 growth rings primitive features in *E. americana*? I find difficulty in assenting because of the distribution of these features elsewhere in the genus. Helical thickenings would probably appeal as a specialization *a priori* to some workers, and in view of the occurrence of this feature in habitats more extreme for the genus, I would probably be inclined to agree. We cannot use vessel element length as a kind of measuring stick by which to judge degree of phyletic advancement of other features in the wood of *Ephedra* as we can in dicotyledons: in gymnosperms, tracheary element length relates to plant or organ size, not phyletic status (Carlquist 1975). We cannot use degrees of perforation plate simplification as a phyletic indicator in *Ephedra,* as we can in dicotyledons and monocotyledons: the number of perforations, the only significant variable in this respect in *Ephedra,* is governed by vessel diameter, which varies with respect to ecology and position of a vessel in a growth ring. Vessel element length is correlated primarily with ontogeny in *Ephedra,* also with plant size (which usually relates closely to age of plant, although not in shrubs of high alpine situations). There is no reason to believe that length of vessel elements in *Ephedra* is in any way conservative or irreversible, and thereby it cannot be a useful phyletic indicator.

In order to assign polarity to the character states of anatomical features, we would very likely have to do a total cladistic analysis of the genus. There are a few distinctive features, such as the fleshy or dry bracts of female strobili, or the presence of leaves in threes or in pairs. However, even the gross morphological characters may not be as readily used for phyletic analysis as in some other groups. If *Ephedra* is ancient, sufficient time for particular features to have evolved more than once has occurred, and the "missing links," so useful in analysis of recently evolved clades, are fewer. By placing the *Ephedra* species with dry bracts before those with fleshy bracts, Stapf (1889) presumably regards the former as more primitive, but there is no compelling reason for this treatment, and even if one agrees with it one has no way of knowing, from distribution of other characters, whether fleshy bracts evolved once, a few, or many times. Professor Helmut Freitag of the University of Kassel, working with vegetative anatomy in an attempt to find taxonomic characters, says, "we tried to make use of anatomical characters, but unfortunately we were not much more successful than Stapf. We found a few rather reliable characters, but not sufficient to produce a working key" (Freitag, personal communication).

Very likely, phylesis within the genus can be elucidated only by chemical studies. When chemical studies are available, the phyletic status of particular anatomical characters as well as the bract texture, leaf number, habitat type, and other features may become clearer. Because of the highly disjunct nature of the genus, accumulation of suitable material for a thorough analysis of the genus with respect to secondary products as well as genetic material will not be easy.

In recent years, the concept that Gnetales might be close to angiosperms has been revived (Muhammad and Sattler 1982; Crane 1985; Doyle and Donoghue 1986). Thompson (1912), on the basis of wood and other anatomical features, and various workers, on the basis of strobilar morphology and anatomy and on the anatomy of the life cycle (see Martens 1971), concluded that Gnetales offer

many parallelisms to angiosperms, but are not closely related to them. The tracheids of *Ephedra* are like the tracheids of conifers (and other gymnosperms) in a number of salient respects (bordered pits large, circular, pit membranes with thick torus central to a margo composed of an open mesh of strands). The vessels of *Ephedra* are clearly derived from such tracheids (Bailey 1944). A striking feature, not often mentioned, but found in *Ephedra* and other Gnetales as well as in conifers is the intercalation of bordered pits into the gyres of primary xylem helical tracheids. This phenomenon is unknown in angiosperms, Cycadales, and Cycadeoideales.

Uniseriate rays are infrequent in *Ephedra,* with the exception of a few species, whereas in dicotyledons, uniseriate rays are always present in woods with the most primitive ray type, Heterogeneous I of Kribs (1935). I do not find any compelling reason to say what the primitive ray type in *Ephedra* might be, although multiseriate rays, present in all species, must have been present in the ancestors of *Ephedra.* In only a few species of *Ephedra* are there cells that could be called strands of axial parenchyma. In most *Ephedra* woods, I was able to find only the nucleated cells I am terming fiber-tracheids. Thompson (1912) regards these fiber-tracheids as the product of a kind of tracheid dimorphism, an interpretation I find entirely plausible on account of their pitting features, wall thickness, and lack of septation or subdivision into strands. If this interpretation is correct, wood of *Ephedra* is primitively devoid of axial parenchyma, whereas axial parenchyma is present in all phylads of primitive dicotyledons. Thus, there are some clear discontinuities between wood of *Ephedra* (and other Gnetales) and wood of dicotyledons.

The presence of minute calcium oxalate crystals on the outer surfaces of wood and bark cells in *Ephedra* is so pervasive within the genus, despite the fact it was not mentioned prior to my 1989 paper, that one must consider it a basic feature of *Ephedra.* These minute crystals were known in leaf epidermis, and also occur in the stem epidermis, apparently in the cuticle (see Fig. 45). I believe the presence of these crystals might be considered indicative of relationship to *Welwitschia,* the peculiar "spicular cells" of which, found throughout the plant body, bear similar coverings of calcium oxalate crystals. These cells are likely described by Parameswaran and Liese (1979), who give a good review. A few instances of cells covered with minute calcium oxalate crystals are known in angiosperms (notably foliar sclereids of Nymphaeaceae and Schisandraceae: Metcalfe and Chalk 1950). However, the majority of instances of cells covered with minute calcium oxalate crystals are in conifers, such as leaves of *Araucaria* (Griffith 1950) and bark of Cupressaceae (Sinz 1925; Wallendorff and Meier 1970), instances in which the mode of occurrence of these crystals is like those of Gnetales. This feature is worthy of more investigation, perhaps using transmission electron microscopy as done by Oladele (1982).

Some features of *Ephedra* wood do resemble those of dicotyledon wood, but one can explain these are features that show similarity for functional reasons, not for reasons of common descent. For example, in rays, the proportion of procumbent cells increases over time, just as it does in dicotyledons. However, procumbent cells are theoretically more efficient at radial conduction of solutes than upright cells, so that predominance of procumbent cells in wider stems is physiologically understandable. Likewise, the grouping of the nucleated fiber-tracheids into a

tangential "diffuse-in-aggregates" configuration provides bands of living cells that interconnect rays, and offers interconnection between these vertical cells and horizontal cells (rays), thereby linking the two photosynthate-containing systems. Even the occurrence of borders on ray cell pits of *Ephedra* and of dicotyledons has a similar potential explanation, that of facilitating photosynthate translocation. The systematic occurrence of bordered pits in ray cells of dicotyledons does not suggest they are primitive for the group: they occur in a wide range of groups, and their occurrence seems related to ray physiology entirely.

The above examples illustrate that elucidation of relationships of Gnetales does not appear to be simplifying at all. Because Gnetales are a smaller group than angiosperms, and because very few fossils are known (Crane and Upchurch 1987), origin of Gnetales appears to be an even more abiding mystery than the "abominable mystery" of angiosperm origin, despite the attention the latter has attracted.

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LITERATURE CITED

Baas, P. 1973. The wood anatomical range in Ilex (Aquifoliaceae) and its ecological and phylogenetic significance. Blumea 21:193–258.

Bailey, I. W. 1923. The cambium and its derivative tissues. IV. The increase in girth of the cambium. Amer. J. Bot. 10:499–509.

———. 1944. The development of vessels in angiosperms in morphological research. Amer. J. Bot. 31:421–428.

———, and W. W. Tupper. 1918. Size variation in tracheary cells. I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms, and angiosperms. Proc. Amer. Acad. Arts 54:149–204.

Bobrov, E. G. 1968. Ephedraceae, pp. 154–160. *In* V. L. Komarov [ed.], Flora of the U.S.S.R., Vol. 1 (translated from Russian). Israel Program for Scientific Translations, Jerusalem.

Carlquist, S. 1966. Wood anatomy of Compositae: a summary, with comments on factors controlling wood evolution. Aliso 6(2):25–44.

———. 1969. Wood anatomy of Lobelioideae (Campanulaceae). Biotropica 1:47–72.

———. 1975. Ecological strategies of xylem evolution. Univ. Calif. Press, Berkeley and Los Angeles. 259 p.

———. 1980. Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. Aliso 9:499–553.

———. 1982. Wood anatomy of *Illicium* (Illiciaeceae): phylogenetic, ecological, and functional interpretations. Amer. J. Bot. 69:1587–1598.

———. 1988. Near-vessellessness in *Ephedra* and its significance. Amer. J. Bot. 75:596–599.
———. 1989. Wood and bark anatomy of the New World species of *Ephedra.* Aliso 12:441–483.
Carlquist, S., and S. Zona. 1988. Wood anatomy of Papaveraceae, with comments on vessel restriction patterns. IAWA Bull., n. s., 9:253–267.
Crane, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. Ann. Missouri Bot. Gard. 72:716–793.
———, and G. R. Upchurch, Jr. 1987. *Drewria potomacensis* gen. et spec. nov., an early Cretaceous member of Gnetales from the Potomac Group of Virginia. Amer. J. Bot. 74:1722–1736.
Danin, A., and I. C. Hedge. 1973. Contributions to the flora of Sinai. I. New and confused taxa. Notes Roy. Bot. Gard. Edinburgh 32:259–271.
Doyle, J. A., and M. J. Donoghue. 1986. Relationships of angiosperms and Gnetales: a numerical cladistic analysis, pp. 177–198. *In* B. A. Thomas and R. A. Spicer [eds.], Systematic and taxonomic approaches in palaeobotany. Oxford University Press, Oxford.
Ewers, F. W. 1985. Xylem structure and water conduction in conifer trees, dicot trees, and lianas. IAWA Bull., n.s., 6:309–317.
Fahn, A., E. Werker, and P. Baas. 1986. Wood anatomy and identification of trees and shrubs from Israel and adjacent regions. The Israel Academy of Sciences and Humanities, Jerusalem. 221 p.
Greguss, P. 1955. Identification of living gymnosperms on the basis of xylotomy. Akademiai Kiado, Budapest. 263 p.
Griffith, M. M. 1950. A study of the shoot apex and leaf histogenesis in certain species of *Araucaria.* Thesis, University of California, Berkeley.
Kribs, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. Bot. Gaz. (Crawfordsville) 96:547–557.
Kukachka, B. F. 1977. Sectioning refractory woods for anatomical studies. U.S. Forest Service Res. Note FPL 0236:1–9 (also Microscopica Acta 80:301–307, 1978).
Martens, P. L. 1971. Les gnétophytes. Handbuch der Pflanzenanatomie 12(2):1–295. Gebruder Borntraeger, Berlin and Stuttgart.
Metcalfe, C. R., and L. Chalk. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford. 1500 p.
Muhammad, A. F., and R. Sattler. 1982. Vessel structure of *Gnetum* and origin of angiosperms. Amer. J. Bot. 69:1004–1021.
Oladele, F. A. 1982. Development of the crystalliferous cuticle of *Chamaecyparis lawsoniana* (A. Murr.) Parl. (Cupressaceae). Bot. J. Linn. Soc., 84:273–288.
Parameswaran, N., and W. Liese. 1979. Crystal-containing walls of spicular cells in *Welwitschia.* IAWA Bull. 1979/4:87–90.
Riedl, H. 1963. Ephedraceae, pp. 1–8. *In* K. H. Rechinger [ed.], Flora Iranica. Akademische Druck- und Verlagsanstalt, Graz, Austria.
———. 1980. Notes on *Ephedra.* Notes Roy. Bot. Gard. Edinburgh. 32:291–295.
Sinz, P. 1925. Calciumoxalat-Kristalle als Bausteine im mechanischen System der Cupresssineen-rinde. Bot. Arch. 10:10–16.
Stapf, O. 1889. Die Arten der Gattung Ephedra. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 56(2):1–112.
Thompson, W. P. 1912. The anatomy and relationships of the Gnetales. I. The genus *Ephedra.* Ann. Bot. 26:1077–1104.
———. 1918. Independent evolution of vessels in Gnetales and angiosperms. Bot. Gaz. (Crawfordsville) 65:83–90.
Wallendorff, J., and H. Meier. 1970. Zur Bildung von Kalziumoxalatkristallen in der Zellwanden der Rinde von Cupressaceae. Verh. Schweiz. Naturf. Ges. 1970:240–242.